Observations on the Myology of *Dugong dugon* (Müller)

DARYL P. DOMNING

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ABSTRACT

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Though closely paralleling cetaceans in swimming adaptations, sirenians are much less specialized in this regard, since they are not active predators. Manatees show less anatomical specialization and presumably less efficiency and endurance in swimming than dugongs because manatees are less active and inhabit more protected waters. The structure of the shoulder region is quite different in the two sirenian families and may reflect the requirements of maneuvering in more or less open habitat. Other muscle systems, however, are not notably different in the two families.

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Introduction

Very little of the considerable research done to date on the anatomy of the living sirenians has been devoted to their muscular systems. The principal, and almost the only, treatment of sirenian myology is found in James Murie's treatises (1872, 1880) on the gross anatomy of the manatee. Bahrdt (1933) redescribed some limb muscles of the manatee, Slijper (1946) commented upon some details of the back muscles, and other authors contributed observations on visceral or skeletal muscles in describing other organ systems; but, so far as I am aware, the only attempt at describing the sirenian muscular system as a whole is that of Murie.

In order to investigate the differences in functional myology between manatees and dugongs and between sirenians and other marine vertebrates, and to have some basis for understanding the functional adaptations of extinct dugongids, it is first necessary to gain at least as much knowledge of the myology of *Dugong* as Murie has given us for *Trichechus*. This is the aim of the present study.

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Materials, Methods, and Terminology

The dissection was performed on an immature female dugong (Dugong dugon (Müller) Palmer, USNM 307611) captured in the Palau Islands in June 1957 by the George Vanderbilt Foundation of Stanford University. The specimen was preserved in formalin and weighed about 300 pounds when fresh. Its second molar was worn and the third molar unerupted. Since this description is based on only the left side of one individual, and hence is subject to all the limitations which that implies, this account should in no way be taken as definitive. I have cited all the significant statements in the literature known to me bearing on each muscle

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of either manatee or dugong. All comparisons with the manatee are, unless otherwise stated, based on Murie's (1872, 1880) accounts of three specimens of *Trichechus manatus manatus* Linnaeus. I have usually omitted comparisons with the manatee, however, where its anatomy agrees with that of the dugong. Measurements taken at the time of dissection (June 1971) are given in Table 1.

Unfortunately, time did not permit investigation of muscle innervation, so the homologies I suggest are based only on gross relations. Quotation marks denote names I have coined or used in other than the usual fashion. Question marks before muscle names denote doubtful identification.

The illustrations are semidiagrammatic and with a few exceptions all structures other than muscles and bones are omitted. The directions of the muscle fibers are indicated by solid lines and tendinous or aponeurotic fibers by dashed lines. Origins are denoted by patterns of circles, insertions by patterns of vertical dashes. The abbreviations beginning with capital letters refer to muscles and those beginning with lower-case letters refer to other structures; all are explained in the "List of Abbreviations."

TABLE 1.-Measurements (cm) of immature female Dugong dugon (USNM 307611) from Palau Islands

т		No.	01.5
Trunk		Distance between ears (through head)	
Total length, snout to caudal notch	185	Distance between ears (over top of head)	
Girth, neck just behind vertex of cranium	78	Distance, tip of snout to ear	30
Girth, just in front of flippers	99	Diameter of ear opening	0.3
Girth, just behind flippers	103		
Girth, about 85 cm behind snout (maximum girth)	121	FLIPPERS	
Girth at anus	102		
Minimum girth of peduncle	39	Distance, tip of snout to anterior insertion of	
6		flipper	40
HEAD		Distance between tips of outstretched flippers	103
ПЕЛЬ		Distance between insertions of flippers (through	
Length, tip of snout to vertex of cranium	33	body)	
Girth, anterior end of snout and mandible	71	Distance between insertions of flippers (over back)	59
Girth at eye, behind chin	66	Length, anterior insertion to tip*	32
Girth at eye, including chin	73	Length, axilla to tip*	
Length, side of mouth	8	Maximum width*	
Length, lower lip, angle to angle around front		Maximum thickness (at proximal end)*	
of mouth	24	Thickness at metacarpals*	3.3
Width, lower jaw, transversely between angles of		Girth at insertion•	27
mouth	11	Girth at middle*	27
Height, lower jaw, anterior side of lip to ventral		Girth 1/3 of length from tip*	28
tip of chin	12.5		
Width, anterior end of muzzle	18	TAIL	
Height, anterior end of muzzle (not including			
upper rostral pad)	12	Length, anterior edge of fluke to caudal notch	
Distance, dorsal tip of muzzle to nostrils	7	Width across flukes, tip to tip	53
Width across both nostrils	5	Distance, caudal notch to nearest point on anterior	
Width of each nostril	2	edge of left fluke	22
Height of each nostril	1.5	Distance, tip to notch, along posterior edge of	
Diameter of eye	1	left fluke	32.5
Distance, tip of snout to eye	19		
Distance, lateral side of nostril to eye	15	GENITAL ORGANS**	
Distance, angle of mouth to eye	11		
Distance between eyes (through head)	18.5	Distance, anus to caudal notch	60
Distance between eyes (over top of head)	26	Distance, anus to vulva	6
Distance, eye to ear	11	Length, teat	1

[•]Left flipper

^{**} Damage to specimen in ventral midline prevented location of umbilicus.

Discussion of Skin Thickness

Measurements of skin thickness (including both epidermis and cutis) are given in Table 2 and Figure 1 for comparison with the data of Matthes (1929) on sirenian skin thickness. The distribution of thickness differs in several respects from that in Matthes' young Trichechus senegalensis, in addition to the dugong's hide being in general proportionately thicker than the latter's. The dugong's skin is thickest on the back rather than on the side; on the chest at the level of the flipper it thins less than in the manatee; and, in contrast to the manatee, there is a conspicuous thickening on the dorsal

side of the peduncle (less so on the ventral side). The latter feature clearly parallels the similar development in the dorsoventrally expanded peduncles of whales. The epidermis is, as often described, very thin in comparison to the cutis.

There was no development of blubber in the animal under study; the cutis lay directly upon the superficial muscles and aponeuroses. The animal was in general very lean, the most conspicuous deposits of fat lying just forward of and behind the shoulder joint beneath the dermal muscles, and between the cutaneus trunci and the deeper muscles on the side of the thorax.

TABLE 2.—Thickness of skin of immature female Dugong dugon (USNM 307611) measured (in mm) at 10 cm intervals from head to tail

	head																			tail
Area measured	0	10	20	30	40	50	60	70	80	90	100	110	120	130	140	150	160	170	180	185
Dorsal midline		9	9	18	20	20	21	24	23	22	21	19	17	16	22	21	17		_	
Middle of left side		5	8	12	7	9	11	14	14	12	12	12	12	12	10	8	9	_	_	_
Ventral midline		_	13	9	12	12	10	14	12	10	10	10	10	7	7	8	10	6	_	_
					x-		ĸ							t						
	flipper								anus								flukes			

Myological Descriptions

MUSCLES OF THE SUPERFICIAL NECK AND FACE REGION

M. SPHINCTER COLLI SUPERFICIALIS (SpC: Figures 2, 4–6, 18, 19, 22, 32, 33) [Murie, 1872:164, figs. 8, 9, 13, 30: "platysma myoides, P.c 3"].—Coarse and fat-veined as Murie described; thins dorsally from a maximum thickness of 1.5 cm over the chest.

Origin: Anteriorly, from midventral line with fellow of opposite side; posteriorly line of origin diverges laterally to a point ventral to axilla, the fibers arising by small separate tendons from fasciae over chest. On the muscle's deep side a few fibers arise from surface of sphincter colli profundus pars auris just medial to shoulder. In midventral line at level of axilla, in V-shaped space formed by divergence of lines of origin of the muscle, there is a

small squarish sheet of coarse fibers; since this lies in chest fasciae in same plane as sphincter colli superficialis and its fibers run in same direction, it may be regarded as a division of the latter.

Insertion: Passes dorsolaterally, radiating slightly, covering throat and shoulder and overlapping lower edge of pars jugularis of platysma; inserts onto hide at side of neck and front of shoulder. Overlies supraspinatus, not infraspinatus as stated by Murie. I did not observe any slip passing onto forelimb as in the manatee (Murie, 1872, fig. 13: "P.c. 3*").

M. PLATYSMA.—I apply this term to the entire thin sheet of muscle which covers the cheek, neck, and anterior shoulder regions just beneath the skin. It has 3 major divisions:

—"PARS JUGULARIS" (PIJ: Figures 2-6, 11, 13, 18, 19, 32, 34).—Continuous sheet including parts

sometimes distinguished as platysma myoides, pars buccalis, and pars mentalis. Coarse-fibered and veined with fat.

Origin: Anteriorly, from fascia connected with hide over after edge of levator nasolabialis; more ventrally its fibers are mingled with those of orbicularis oris all around corner of mouth, and a few arise from surface of mentalis. Passes back as most superficial layer of cheek, though at throat its ventral border is overlapped by sphincter colli superficialis. Dorsally arises, together with frontalis and sphincter colli profundus pars auris, by aponeurosis from side of jugal posteroventral to orbit.

Insertion: Passes back into superficial fascia over forward part of shoulder, the more ventral fibers reaching level of axilla; each bundle of fibers terminates in a small, separate tendon, which is lost in fascia. Dorsal fibers sweep up and back to mingle with those of pars temporalis, and some attach to anteroventral side of auditory canal along with those of auricularis profundus.

—"PARS TEMPORALIS" (PIT: Figures 2-4, 11, 18).—May correspond to platysma cervicale of other mammals. Very thin, coarse, fat-veined sheet covering back of neck.

Origin: Superficial fascia over temporal fossa.

Insertion: Mingles ventrally with other parts of platysma and passes back into superficial fascia over anterodorsal part of scapula.

—"PARS SCAPULARIS" (PlS: Figures 2-4, 18-20, 43, 44).—Somewhat fusiform sheet, fibers less coarse than in pars jugularis.

Origin: By small separate tendons from among and mainly beneath dorsal fibers of pars jugularis and ventral fibers of pars temporalis.

Insertion: By single tendon onto fibrous raphe joining trapezius and deltoideus over infraspinatus, attaching to raphe 2.5 cm forward of after edge of deltoideus.

There are two smaller muscles related to the platysma which may or may not be homologs of normal mammalian postauricular muscles:

"M. AURICULARIS SUPERFICIALIS" (AuS: Figures 2, 4, 18).—Small but conspicuous muscle posterodorsal

to ear, about 2 cm long; fibers less coarse than in pars jugularis.

Origin: Surface of pars temporalis near its ventral edge.

Insertion: Passes over insertion of frontalis and around back of auditory canal to insert on latter's posteroventral side.

"M. AURICULARIS PROFUNDUS" (AuP: Figure 11).— Small fusiform bundle 4.5 cm long and 1 cm wide lying on deep side of pars temporalis dorsal to dorsal edge of pars jugularis and diverging from latter posteriorly. Lies in same plane as pars jugularis and clearly derived from it. Also lies approximately parallel to auricularis superficialis. Passes superficially to a bowling-pin-shaped bar of cartilage 1.5 cm long lying posteroventral to auditory canal, pointing anteroventrally, and having no direct muscular or skeletal attachments.

Origin: Fasciae on deep side of pars temporalis, 2 cm behind rear end of zygomatic process.

Insertion: Partly tendinous, together with fibers of pars jugularis, onto anteroventral side of auditory canal.

The pars jugularis evidently corresponds, in the manatee, to the anteriormost parts of Murie's "panniculus carnosus" (Murie, 1872, figs. 8–10, 12: "P.c¹" and part of "P.c²"); the other divisions, including the auriculares, seem to have no trichechid homologs. On the other hand, the portion of Murie's (1872) "P.c²" that he shows coming from the underside of the jaw up to the angle of the mouth is absent in the dugong.

M. SPHINCTER COLLI PROFUNDUS.—

—?PARS AURIS (Au: Figures 5, 6, 13, 19, 22, 23, 32–35) [Murie, 1872:163–164, figs. 8, 9: "panniculus carnosus, P.c²"; Murie, 1880: pl. 8, fig. 5]: Remarkably massive, up to 4 cm thick; covers ventrolateral side of neck and anterior part of chest just beneath sphincter colli superficialis.

Origin: Fleshy and tendinous from ventral side of sternum, from origin of sternomastoideus (here continuous with it) to posterior end of bone, meeting its fellow along midline. Posteriorly mingles with and partly overlies cutaneus trunci, arising from its surface by fasciae and small tendons; for the more lateral connections of the two muscles, see description of cutaneus trunci.

Insertion: Passes beneath frontalis and pars jugularis of platysma and superficial to masseter to insert by very strong aponeurosis onto ventrolateral NUMBER 226 5

side of zygomatic process of squamosal, lower part of lateral side of jugal, and fasciae anteroventral to jugal beneath palpebralis. (This aponeurosis is really a deeper division of that from which frontalis and jugularis arise.) Deep side of auris is tendinous where it passes over masseter.

-PARS INTERMEDIA.

?M. FRONTALIS (Fr: Figures 2, 4–6, 11, 18, 19, 32, 34).—Small triangular muscle just forward of ear; fibers less coarse than in pars jugularis of platysma and at most 6 cm long.

Origin: Aponeurotic from zygomatic process adjacent to pars jugularis of platysma; anteroventrally overlaps latter. Fibers begin in aponeurosis 4 cm forward of ear opening.

Insertion: Passes beneath auricularis superficialis and dorsal to ear to mingle with fasciae between partes jugularis and temporalis of platysma.

M. ORBICULARIS OCULI (OOc: Figures 3, 4, 7) [Murie, 1872:195, fig. 8: "orbicularis palpebrarum"].—Fibers completely continuous around posterior angle of eyelids, though still divided into dorsal and ventral portions anteriorly. Otherwise normal. Pütter (1902:180) stated that in one manatee the ventral part was better developed; I did not observe this, nor did Pütter (1902:185) attribute it to his dugong.

I did not dissect the muscles of the eyeball. Pütter (1902:179–180, 185, 371) attributes to both the manatee and dugong no features out of the ordinary except that the musculi recti all take their origins behind the optic foramen rather than around it.

M. LEVATOR NASOLABIALIS (LeN: Figures 3-6, 12, 13) [Murie, 1872:149, figs. 8, 10, 12: "levator labii superioris alaeque nasi"].—Most superficial of snout muscles; fan-shaped, its fibers radiating forward and predominantly anteroventral in direction.

Origin: Tendinous from anterolateral edges of jugal and lacrimal and dorsal side of supraorbital process of frontal to as far back as level of latter's posterolateral corner.

Insertion: Mingles with fibrous tissue, other muscle fibers, and hide dorsolateral to external nares and down along front of snout to upper lip, where it mingles with platysma and orbicularis oris. None of these are separable at front of snout, but fuse into a homogeneous mass of isolated fibers in a matrix of fibrous tissue underlying hide and adherent to premaxillae. Near nares, however, levator

nasolabialis does not closely approach midline or connect with fellow of opposite side as in the manatee.

—PARS PALPEBRALIS (Plp: Figures 4-7).—Divided into a larger anterior and a smaller posterior group of very loosely connected bundles of coarse fibers. Not found in the manatee.

Origin: From hide about 4 cm below eye.

Insertion: Passes beneath pars jugularis of platysma to tendon (in common with mandibularis, p. 6) posteroventral to angle of mouth.

-PARS ORALIS.-

M. ORBICULARIS ORIS (OOr: Figures 4-7) [Murie, 1872:150, figs. 10, 11].—Chief component of lips. Discontinuous at angle of mouth, where dorsal part overlaps ventral without continuity of fibers. Less developed on lower lip. Mingles extensively with platysma, buccinatorius, and levator nasolabialis; closely adherent to hide.

M. BUCCINATORIUS (Bu: Figures 5, 6, 9, 10, 13, 14, 16, 17, 24, 25) [Murie, 1872:150, figs. 10, 11].— Prominent, thick muscle of cheek, immediately in contact with inner side of mouth. Has two closely adherent layers: Superficial layer (pars buccalis) is posteroventral in direction and covers posterior part of deep layer; a few isolated fibers pass anteroventrally across anterior part of deep layer. Deep layer (pars molaris) is still more anteroventral in direction, and mingles with fibers of orbicularis oris on upper lip; not distinct or separable from it on lower. Fleshy origin from entire lateral and alveolar borders of premaxilla and maxilla from near tip of rostrum back to end of tooth row (here associated with retractor labiorum); and from alveolar border of mandible, anteriorly by shiny tendinous sheet passing anteromedially to 2 cm ahead of tooth row, and posteriorly fleshy from anteromedial side of base of ascending ramus.

M. MAXILLONASOLABIALIS (Mnl: Figures 5, 6, 13, 14) [Murie, 1872:148, figs. 8, 10, 11, 12: "levator labii superioris proprius"].—According to Miller, et al. (1964:135), this muscle actually homologous to levator labii superioris alaeque nasi of primates. Second layer of snout muscles, beneath levator nasolabialis; likewise fan-shaped and radiating forward but more horizontal in direction than latter, with some fibers even passing anterodorsally. Fibers coarse, rather loosely connected; covered by thick blanket of fasciae.

Origin: Tendinous from a strip of about 4 cm

along anterior side of jugal, medial to levator nasolabialis.

Insertion: Mingles with other muscle fibers and fibrous tissue at anterior end of snout.

M. LATERALIS NASI (LaN: Figures 5, 6, 12, 13) [Murie, 1872:148-149, figs. 11, 12: "levator anguli oris," "depressor labii superioris alaeque nasi," and/or "zygomaticus" (not equivalent to zygomaticus of other animals)].-Third and deepest layer of snout, continuous dorsally with muscle mass lying within mesorostral fossa between premaxilla and nasal passage. May represent an anterior and lateral expansion of what corresponds to pars ventralis m. lateralis nasi in, for example, the horse, and its modification into a major unit of snout system; or may be an expanded dilatator nasi. Modified anterolateral part of muscle may be regarded separately as follows: Fibers pass anterodorsally; ventral part traversed by large bundle of nerves and vessels issuing from infraorbital foramen.

Origin: Fleshy from most of lateral surface of premaxilla; maxilla exposed behind it.

Insertion: Like overlying layers, becomes lost in muscle and tissue mass at front of snout. Dorsally, fibers less distinct and mixed with much fibrous tissue; muscle extends into mesorostral fossa to occupy its normal position.

In the muscle mass occupying the mesorostral fossa I recognized two parts, inseparable and distinguished only by different direction of fibers: first, fibers scattered in fibrous tissue over narial passages, mostly transverse and attached to hide (perhaps representing M. transversus nasi (TrN: Figure 3)); second, a thick muscle with origin on dorsomedial side of frontal process of premaxilla and insertion on ventrolateral side of nasal passage (lateralis nasi). Latter extends from rear of mesorostral fossa to diminish and lose itself in tissue at front of snout, and is continuous with sheet-like portion on lateral side of premaxilla described above. These two parts within mesorostral fossa may correspond, respectively, to Murie's "compressor nasi" plus "dilatator naris", and "pyramidalis nasi" (1872:148, figs. 10-12).

?M. MENTALIS (Mt: Figures 4-7, 16) [Murie: 1872:150, figs. 8, 9, 10, 11: "depressor labii inferioris"].—Covers side of mandibular symphysis beneath platysma, which sends a few fibers onto its surface near its rear edge. Mandibularis tendon

pierces it from beneath and emerges onto its surface about 1.5 cm from its rear edge. Not connected to fellow of opposite side as in manatee, but separated from it by about 1 cm of thick fibrous tissue.

Origin: Fleshy from lateral side of symphysis from dorsal border adjacent to second and third incisor alveoli (and beneath orbicularis oris) down to ventral extremity of symphysis; vessels from mental foramen, however, pass beneath it.

Insertion: Onto hide at lower corner of symphysis. Its attachments are the reverse of those of the seemingly corresponding muscle in the manatee, causing it to pull up on the hide at the chin rather than down at the lip.

The muscle Murie (1872:149, fig. 9) termed "levator labii inferioris" is absent in the dugong; the front of the mandible is covered by a thick pad of fasciae containing a very few transverse muscle fibers, probably derived from the orbicularis oris.

"M. RETRACTOR LABIORUM" (ReL: Figures 6, 7, 9, 10, 14, 25).—Strap-like, 1 cm wide, lying directly on lateral surface of mandible beneath palpebralis. Without homolog in manatee. Does not seem to correspond to a normal zygomaticus, and is perhaps a derivative of buccinatorius.

Origin: Fleshy, nearly inseparable from buccinatorius, at posterodorsal edge of latter's origin on maxilla at rear of tooth row.

Insertion: Tendinous into fibrous tissue and fibers of orbicularis oris at angle of mouth.

M. MANDIBULARIS (Mn: Figures 5-7, 10, 17, 33) [Murie, 1872:151, fig. 11].—Approximately as in manatee; long, narrow, and strap-like. Perhaps a derivative of buccinatorius.

Origin: Tendinous from small area on anteromedial side of base of ascending ramus of mandible, posterodorsal to coronoid canal (= large foramen at rear of lower tooth row).

Insertion: By tendon passing ventrolaterally through mentalis onto hide on anteroventral side of mandibular symphysis. Palpebralis joins this tendon just behind mentalis. Tendon does not join fellow of opposite side.

M. DEPRESSOR ANGULI ORIS (DAO: Figures 4, 5) [Murie, 1872:150, figs. 8-10].—This muscle, well developed in *Trichechus*, may be represented vestigially in *Dugong* by, first, a few fibers embedded in anterior tendon of mandibularis where it is exposed on surface of mentalis; and, second, a small thin tendon emerging from surface of men-

talis near its after edge just ahead of palpebralis tendon, passing upward parallel to latter, and becoming lost in fasciae and fibrous tissue near angle of mouth. Incorporation of depressor anguli oris fibers into the mandibularis-palpebralis tendon results in the unusual situation of three muscles pulling in divergent directions on a single tendon.

Muscles of the Jaws

M. MASSETER (M: Figures 5-8, 10, 13, 14, 16, 23, 34) [Murie, 1872:151, figs. 10, 30: "masseter, Ma1"].—Covers side of posterior half of mandible beneath sphincter colli profundus pars auris. Crossed by numerous nerves and vessels and superficially sheathed in shining tendon towards origin. On deep side near origin it is partly divided; deep division smaller (about 4 cm wide) than other, with more vertically oriented fibers, and fused with superficial part anteriorly and ventrally. Both divisions contain parallel tendinous sheets which join the superficial sheath.

Origin: Tendinous on superficial side and fleshy deeper, from ventral and posteroventral edges of jugal back to behind level of tip of squamosal, and anteromedially on jugal as far as maxillary suture.

Insertion: Fleshy on whole posteroventral half of posterior part of mandible, especially on latter's posteroventral edge.

M. ZYGOMATICOMANDIBULARIS (Z: Figures 3, 6-14, 16) [Murie, 1872:151, fig. 11: "masseter, Ma²"].— Deep to masseter (though exposed posterodorsal to it) and separated from it by a large mass of blood vessels passing forward from rear edge of mandible. Its fibers pass nearly at right angles to those of masseter, as in *Trichechus*. Covered by shining fascia near insertion, and considerably larger than temporalis.

Origin: Tendinous from strip about 2 cm long on ventrolateral edge of zygomatic process of squamosal adjacent to posterior end of jugal; fleshy from medial side and ventral edge of latter, and whole medial side of zygomatic process; fused posteriorly with temporalis.

Insertion: Fleshy on anterior half of ascending ramus and coronoid process of mandible; fibers coming from ventral edge of zygomatic arch insert in hook-shaped pattern below main insertion.

M. TEMPORALIS (T: Figures 3, 5, 6, 8-10, 12, 13, 17, 19, 20-22) [Murie, 1872:151, figs. 8, 10].—Hid-

den by thick sheet of fascia covering whole temporal fossa. Relatively small, as in manatee, and covered, especially at rear, by shining fascia. Fused posterolaterally with zygomaticomandibularis. Contains a tendinous sheet continuous posteriorly with the superficial sheath.

Origin: Fleshy from lateral side of cranium, covering squamosal dorsal to root of zygomatic process, part of parietal, dorsal wing of alisphenoid, and posteriormost edge of frontal.

Insertion: Tendinous onto rim of coronoid process and fleshy onto its medial side down to a point just posterior to coronoid canal. Only development of a "superficial" division is a fold on anterior edge, which just manages to cover a small part of lateral side of temporalis tendon; there is no insertion on lateral surface of bone.

M. PTERYGOIDEUS EXTERNUS (PtE: Figures 9, 13, 17, 24, 25) [Murie, 1872:180].—Short, thick; oval in cross-section.

Origin: Fleshy from anteroventral part of lateral surface of pterygoid process.

Insertion: Fleshy into pterygoid fossa anteroventral to condyle on medial side of ascending ramus of mandible.

Turnbull (1970:349) alluded to "peculiarities" of the temporalis and pterygoideus externus in sirenians. He has informed me that he was referring to the apparent (from osteological materials) absence of a superficial temporalis (probably represented at least in part by the zygomaticomandibularis) and large size of the pterygoideus externus (confirmed by this dissection).

M. PTERYGOIDEUS INTERNUS (PtI: Figures 9, 10, 13, 14, 17, 24, 25) [Murie, 1872:180].—Wide and fanshaped; complexly pinnate.

Origin: Fleshy and tendinous from posterolateral side of pterygoid process, adjacent and posteroventral to origin of pterygoideus externus.

Insertion: Fleshy and tendinous on whole posteroventral part of medial side of mandible.

M. DIGASTRICUS (Di: Figures 6, 8-10, 17, 23-25, 31, 34) [Murie, 1872:180, figs. 9, 10, 30; 1880, pl. 8: fig. 5].—As in manatee, consists of only one belly (anterior).

Origin: Fleshy from lateral sides of stylohyoid and epihyoid; no fibers attach to skull.

Insertion: Fleshy on medial edge of lower half of posterior border of mandible down to its angle, thence about 3 cm anterodorsally along ventro-

medial edge of mandible's ventral border. Does not, nor does any other muscle, completely cover rearfacing flat surface of posterior border, which is primarily produced by stresses of muscles inserting on lateral and medial sides of mandible along its after edge, stimulating bone deposition laterally and medially along the edge.

MUSCLES OF THE MIDDLE EAR

These I did not dissect, but I have gleaned the following information from the literature:

M. TENSOR TYMPANI.—

Origin: From posterior side of bridge connecting tympanic to tegmen tympani (Robineau, 1969:26).

Insertion: Tendinous on processus muscularis on medial side of malleus (Robineau, 1965, fig. 5; 1969, fig. 6).

M. STAPEDIUS .-

Origin: From fossa muscularis minor on underside of petrosal, posterolateral to fenestra ovale (Robineau, 1969:10, figs. 5, 6). This was confirmed by my observation of the remnant of a tendon attached at this point in a dried *Dugong* skull (USNM 197900).

Insertion: Tendinous on posterior side of neck of stapes (Robineau, 1969, fig. 6). Doran (1878:467) states that the site of insertion is usually indicated by a slight depression.

TONGUE AND HYOID MUSCLES

M. STYLOGLOSSUS (Styg $_{1-3}$: Figures 8, 23, 24, 25, 30, 31) [Murie, 1872:180, figs. 18, 37].—Has three divisions, as follows, proceeding ventrally:

—FIRST (Styg₁, Figures 8, 23, 24, 25, 30).—Thickest and strongest division.

Origin: Fleshy from anterolateral edges of stylohyoid and of proximal end of epihyoid.

Insertion: Partly tendinous into posterolateral part of tongue.

—second (Styg₂; Figures 24, 25, 30).—

Origin: Fleshy from anterior side of epihyoid, distal to first division.

Insertion: Into posterolateral part of tongue ventral to first division.

—THIRD (Styg₃; Figures 24, 25, 31).—

Origin: Tendinous from anterolateral edge of epihyoid lateral to second division.

Insertion: Longest division, inserting (partly tendinously) into ventrolateral side of tongue, lateral to genioglossus and hyoglossus.

M. HYOGLOSSUS (Hg: Figures 24, 25, 31).—Thin, about 2.5 cm wide. Not observed by Murie in the manatee.

Origin: From fibrous raphe in midline with its fellow, and fleshy from ventral sides of basihyoid (lateral to other muscle attachments) and (perhaps by a few fibers) thyrohyoid.

Insertion: Passes anterodorsally into tongue, medial to third division of styloglossus.

M. GENIOGLOSSUS (Gg: Figures 17, 24, 25, 30) [Murie, 1872:180: ?"genio-hyo-glossus"].—Thin, lying in parasagittal plane beneath tongue. Converges on and unites with fellow of opposite side posteriorly, merging with fibrous tissue connecting pharynx and rear of tongue.

Origin: Tendinous from fossa on posterodorsal surface of mandibular symphysis.

Insertion: Passes posterodorsally, blending dorsally with fibers of tongue. Posteroventrally, a few fibers insert on dorsal sides of keratohyoids and basihyoid.

The intrinsic muscles of the tongue (Murie's "lingualis", 1872:180) were not dissected. Gudernatsch comments briefly on the muscular structure of the tongues of dugong (1908:601-604) and manatee (1909:185-186).

The sternohyoideus is evidently absent. Murie (1872:179, fig. 9) says "the sterno-hyoid and sternothyroid are interblended" in the manatee, and Stannius (1845:7) says the same; but the absence here of attachments to either the basihyoid or the manubrium seems to leave little ground for asserting its existence at all in the dugong.

Murie (1872:179–180) found an "anterior remnant" of an omohyoideus, but I observed nothing of this sort.

M. THYROHYOIDEUS (Thh: Figures 6, 23–28, 31, 34) [Owen, 1838:38: "thyreo-hyoideus"; Murie, 1872, fig. 9].—Roughly triangular; covers anterolateral side of thyroid cartilage and lies adjacent and parallel to thyrohyoid on latter's posterior side.

Origin: Fleshy from lateral side of lamina of thyroid cartilage.

Insertion: Fleshy onto ventral side of basihyoid between mylohyoideus attachments; no apparent connection with thyrohyoid.

M. MYLOHYOIDEUS (My: Figures 9, 10, 17, 24, 25, 31, 34) [Murie, 1872:180, fig. 30].—Thick, about 4.5 cm wide; forms a sling under deeper intermandibular muscles.

Origin: Fleshy from medial side of mandible, between mandibular foramen and molars.

Insertion: Anterior half joins fellow in midline; posteriorly has fleshy attachment to ventral side of basihyoid, medial to origin of hyoglossus and lateral to thyrohyoideus.

I did not observe a keratohyoideus, but Murie (1872:179) says it is "feebly represented" in Trichechus.

M. GENIOHYOIDEUS (Gh: Figures 17, 24, 25) [Murie, 1872:180].—Forms a thin pouch beneath tongue, open dorsally, and containing a large mass of fasciae and fibrous tissue, which itself seems partly hollow anteriorly. Posteriorly the two sides converge to form rear of pouch, ending in a mass of fibrous tissue.

Origin: Fleshy from crescentic area (concave up) on posterior side of mandibular symphysis, ventral to origin of genioglossus.

Insertion: Ends posteriorly in fibrous tissue connected with anterior edge of hyoglossus, and posteroventrally connected with mylohyoideus. It has here no direct attachment to the basihyoid, though it does in the manatee.

M. STYLOHYOIDEUS (Styh: figs. 24, 25, 31) [Murie, 1872:180, figs. 18, 30, 37].—Rather small and inconspicuous, lying along posterior side of epihyoid and separated from it by several large vessels.

Origin: Fleshy from posterior sides of stylo- and epihyoids at their juncture.

Insertion: Tendinous on posteroventral side of basihyoid.

No distinct jugulohyoideus was observed, though some fibers of the rectus capitis lateralis lie where one would be expected; however, they did not seem to be innervated by any branch of the facial nerve.

MUSCLES OF THE PHARYNX

M. HYOPHARYNGEUS (Hp: Figures 25, 30).—Rather small; partly fused with stylopharyngeus and nearly hidden beneath it. Posteriorly overlain by anterior edge of thyropharyngeus.

Origin: Fleshy from protuberance on medial side of epihyoid, in fusion with stylopharyngeus.

Insertion: With its fellow, on middorsal raphe of pharynx.

M. THYROPHARYNGEUS (Thp: Figures 23, 25-28, 31) [Stannius, 1845:30: ?"thyreoideus transversus"].

—Triangular in outline.

Origin: Fleshy from side of thyroid cartilage dorsal to origin of thyrohyoideus.

Insertion: With its fellow, on middorsal raphe of pharynx, partly overlying posterior edge of hyopharyngeus.

M. CRICOPHARYNGEUS (Crp: Figures 23-31).—

Origin: Fleshy from side of cricoid cartilage and adjacent caudal cornu of thyroid cartilage; on the muscle's posterior edge a small slip arises tendinously from cricoid cartilage just lateral to cricoarytenoideus dorsalis, which passes beneath it.

Insertion: With its fellow, on middorsal raphe of pharynx behind thyropharyngeus. Posterior fibers blend with those of esophagus.

It is not clear to which of these Murie's "constrictores superior and medius" (1872:180, fig. 18) correspond; judging by his figure, the "constrictor medius" seems to be the cricoarytenoideus dorsalis (p. 10), and the "constrictor superior" the combined cricopharyngeus and thyropharyngeus.

M. STYLOPHARYNGEUS (Styp: Figures 25, 30, 31) [Murie, 1872:180, figs. 18, 30].—Well developed, partially divided longitudinally into anterior and posterior halves. Proximal end lies against wall of tympanic cavity. Adjacent and parallel to stylohyoideus; in the manatee, they are "closely adherent."

Origin: Fleshy from medial side of stylohyoid; some connection also to protuberance on medial side of epihyoid together with hyopharyngeus.

Insertion: Into side of pharynx just forward of and partly fused with hyopharyngeus.

A distinct palatopharyngeus was not observed; its fibers are apparently inseparably mingled with those of the hyopharyngeus, stylopharyngeus, and pterygopharyngeus. Murie (1872:180), however, found it "fairly developed," and his palatoglossus also was not observed.

M. PTERYGOPHARYNGEUS (Ptp: Figures 13, 14, 25).—Very short; not distinct posteriorly.

Origin: Fleshy from posterior side of ventral tip of pterygoid process.

Insertion: Passes posteriorly to mingle with hyopharyngeus and stylopharyngeus on dorsal surface of pharynx.

MUSCLES OF THE SOFT PALATE

M. TENSOR VELI PALATINI (TeV: Figures 14, 24, 25) [Murie, 1872:180: "tensor palati"].—Quite robust; lies against anterior wall of tympanic cavity and fills fossa on posterior side of pterygoid process.

Origin: Tendinous from anteromedial edge of tympanic. Sheathed in shining fascia near origin.

Insertion: Into soft palate immediately ventromedial to pterygoid process, by tendon passing anteromedially around trochlear surface of process.

I failed to find a levator veli palatini; Murie's (1872:180) "levator palati" was not very well developed either. The m. palatinus was not dissected.

MUSCLES OF THE LARYNX

M. CRICOTHYROIDEUS (Crt: Figures 23–29, 31) [Owen, 1838:38; Murie, 1872, fig. 30].—Anteroventral and closely adherent to cricopharyngeus.

Origin: Fleshy from ventrolateral side of cricoid cartilage.

Insertion: Fleshy on posterolateral side of thyroid cartilage.

M. CRICOARYTENOIDEUS DORSALIS (CrD: Figures 24–30) [Murie, 1872:180, fig. 18: ?"constrictor medius"].—Covers dorsal side of cricoid cartilage.

Origin: Fleshy from posterior half of dorsolateral surface of cricoid cartilage.

Insertion: Runs anterolaterally around esophagus and beneath cricopharyngeus to fleshy insertion on muscular process of arytenoid cartilage.

M. CRICOARYTENOIDEUS LATERALIS (CrL: Figures 27, 29) [Owen, 1838:38: "crico-arytenoideus"].—Fused with and posterior to thyroarytenoideus.

Origin: Fleshy from anterior edge of cricoid cartilage.

Insertion: Runs nearly vertically to fleshy attachment on underside of muscular process and posterolateral edge of arytenoid cartilage.

M. THYROARYTENOIDEUS (Tha: Figures 26–30) [Owen, 1838:38: "thyreo-arytenoideus"].—Covered by lateral portion of thyroid cartilage.

Origin: Tendinous from near dorsal (internal) midline of transverse part of thyroid cartilage.

Insertion: Fleshy on anteroventral side of muscular process and lateral side of arytenoid cartilage.

M. ARYTENOIDEUS TRANSVERSUS (ArT: Figures 26-30) [Owen, 1838:38: "arytenoideus obliquus and

transversus"].—Lies immediately dorsal to thyroarytenoideus and anterior to cricoarytenoideus dorsalis.

Origin: Fleshy from anterodorsal side of muscular process of arytenoid cartilage.

Insertion: Runs anteromedially to join its fellow between arytenoid cartilage and esophagus. Owen (1838:38) found them attached to "a small round cartilage in the posterior interspace of the arytenoids."

Concerning the above muscles, Murie (1872:179) says only that "each and all of the laryngeal muscles are relatively well developed. The extrinsic laryngeal muscles maintain a fair size, with attachments of the ordinary kind."

?M. HYOEPIGLOTTICUS (He: Figure 26) [Owen, 1838:38: "hyo-epiglottideus"; Stannius, 1845:30; Murie, 1872:179: "hyoepiglottideus"].-This was absent in Murie's manatee, though Stannius found it weakly developed, and Owen identified it in his dugong. I did not observe it in the USNM specimen, but it was present in the larynx of a young male Palauan dugong (California Academy of Sciences 11038) as a thick bundle of fibers, medially situated and apparently undivided, passing steeply posterodorsally to insert into the substance of the epiglottis. It passed close to the front of the thyroid cartilage but did not seem to attach to it; the origin had evidently been on some part of the hyoid apparatus, but this had been cut away and was not preserved. I have included this muscle in the illustration of the National Museum specimen's larynx (Figure 26) to show its position.

M. ARYEPIGLOTTICUS (Ae: Figure 27) [Murie, 1872:179: "aryteno-epiglottideus"].—Possibly represented by a few fibers on outer dorsal surface of pharynx forward of arytenoideus transversus, passing anteroventrally. Not differentiated into superior and inferior parts as in the manatee. (This is also termed "arytenoideus obliquus"; see "M. arytenoideus transversus.")

A thyroepiglotticus was not observed, though a few such fibers were found in Murie's (1872:179) manatee ("thyro-epiglottideus"). The vocalis and ventricularis are evidently absent in both dugong and manatee.

DORSAL MUSCLES OF THE TRUNK

M. SPLENIUS (Spl: figures 5, 6, 13, 15, 19-24)

[Murie, 1872:145, fig. 8].—Triangular, covering dorsolateral side of neck just beneath cervical trapezius. Thin forward, but up to 3 cm thick aft.

Origin: Aponeurosis from dorsal midline of neck (beneath aponeuroses of trapezius and (posteriorly) rhomboideus, though the three aponeuroses are not very well separable) along whole cervical and anterior thoracic region. In the manatee, however, its fibers arise from the surface of the underlying longissimus and semispinalis capitis, to judge by Murie's account.

Insertion: Tendinous onto posterior side of sigmoid ridge of squamosal, posteromedial to cranial origin of trapezius. I think Murie (1872:145) was mistaken in saying it attached to the "exoccipital ridge."

EPAXIAL SPINAL MUSCULATURE

The epaxial muscles of the Sirenia are characterized by extensive fusion, obscuring most of the divisions that are easily observed in land mammals. The extreme shortening of the neck has reduced and simplified the musculature of this region, and the loss of hind limbs has removed the division between trunk and tail muscles, so that there is a single continuous epaxial muscle mass from the occiput to the tip of the tail. This is composed of the transversospinalis and longissimus systems, which are virtually inseparable; the iliocostalis remains distinct.

Transversospinalis System

Apart from the semispinalis capitis, this appears to be composed entirely of multifidus and shorter fascicles, though Slijper (1946:77, 112, table 3) indicates some semispinalis fascicles may also be present; he (1946:78, tables 3, 6) also describes a "spinalis" arising from the skull to the fifth thoracic vertebra and inserting from the seventh to the twelfth, which I failed to find. His specimen, however, was much younger than mine (only 110 cm long), and perhaps the spinalis had become fused with the other epaxial muscles in the older animal. As for the manatee (*T. inunguis*), Slijper indicates the absence of the spinalis and the presence of semispinalis fibers, as well as a stronger development of the transversospinalis relative to the longis-

simus than in the dugong (Slijper, 1946, tables 3, 6). Murie (1872:144, fig. 39) likewise identified semi-spinales in the manatee, and also a "spinalis dorsi" (including "levator caudae internus"), but does not seem to indicate by the latter term a spinalis in the precise sense used by Slijper (1946); rather merely the outer parts of the transversospinalis complex.

The transversospinalis mass in the dugong lies medial to the longissimus and dorsal to the metapophyses of the vertebrae; from about the middle of the thoracic region back it is enclosed between the spinous and metapophysial tendinous sheets of the longissimus (q.v.). It only becomes separable from the longissimus just forward of the base of the flukes, and it extends to the end of the tail. It consists throughout of undifferentiated short muscle fascicles and tendons, none of which appear to span more than four vertebrae (i.e., appear to be semispinalis fibers).

M. SEMISPINALIS CAPITIS (SeC: Figures 3, 12-15, 20-24, 36-39) [Murie, 1872:145, fig. 8: "complexus"].—Thick, encasing back and side of neck just beneath splenius. A short, shallow longitudinal cleft on surface of muscle at about level of atlas and axis is only vestige of a possible division into biventer cervicis and complexus portions.

Origin: Posteriorly continuous with undifferentiated epaxial mass. Along its ventral edge it has fleshy attachments to dorsal side of tip of transverse process of atlas between attachments of rectus capitis lateralis and obliquus capitis caudalis, and to side of postzygapophysis of axis; also arises by tendons from lateral tips of prezygapophyses of cervicals 3–7, and from dorsal sides of transverse processes of thoracics 1–7. (Murie, 1872:145, traced it back to "above the head of the sixth rib.")

Insertion: Fibers pass anteriorly and anterodorsally to insert pinnately on both sides of tendinous sheet, thickened dorsally, which begins about level of third thoracic. Tendon inserts on and covers lateral border of supraoccipital, and is exposed there; ventrally it is covered by fibers of the muscle having fleshy insertion on most of dorsolateral border of exoccipital and on latter's posterior side lateral to condyle, nearly down to top of rectus capitis lateralis insertion. Finally, a fleshy insertion into large nuchal fossa of supraoccipital; this part of muscle overlaps exposed tendon with a fold over latter's posterodorsal side.

Longissimus System

The principal epaxial muscle mass, readily separable into two parts, hardly of comparable importance.

M. LONGISSIMUS CAPITIS (LnC: Figures 6, 13, 15, 20, 22–24) [Murie, 1872:144: "trachelo-mastoid"].—Rather small, straplike; about 3 cm wide, lying ventral and parallel to splenius, and like it overlain posteriorly by shoulder girdle.

Origin: By thin aponeurosis on side of semispinalis capitis, adjacent to and in same plane as a triangular bundle of fibers rooted at rear of cleft between semispinalis capitis and longissimus dorsi. The fibers of the bundle pass anteriorly and become tendinous, but have no apparent direct connection with longissimus capitis.

Insertion: Passes forward across semispinalis capitis, thickening somewhat, to fleshy insertion on posterolateral side of posttympanic process of squamosal. I suspect Murie (1872:144-145) was wrong in saying it inserted on the exoccipital.

M. LONGISSIMUS DORSI (LnD: Figures 3, 22–24, 36–39, 41, 42, 49, 50, 51, 52) [Murie, 1872:144, figs. 8, 39: "transversalis colli" + "longissimus dorsi," including "levator caudae externus"; Slijper, 1946: 47, 74, 75, 76, 112, table 3].—A continuous unit extending from atlas to end of tail. Anteriorly lies ventrolateral to semispinalis capitis, separated from it by cleft extending back as far as third thoracic. This anterior part is so completely continuous with rest of mass that I see no reason to distinguish a separate longissimus cervicis.

Origin: Fleshy and tendinous on after side of transverse process of atlas (dorsal and medial to scalenus and apparently continuous with semi-spinalis capitis origin), side of centrum of axis, and ends of transverse processes of cervicals 3–7. At its attachment on C₇ and along its ventral edge as far back as sixth rib it is fused with iliocostalis. Also has fleshy origins from dorsal sides of transverse processes from first thoracic back into flukes, dorso-lateral sides of neural arches from T₉ back into flukes, and dorsal sides of all ribs inside their angles.

Insertion: Fibers pass posteromedially to insert on strong aponeurosis from level of fourth thoracic back. Aponeurosis at first lies on medial side of muscle, but a little way aft it starts to pick up fibers passing posterolaterally from vertebrae to insert on its medial side, and so comes to lie in midst of muscle about halfway between neural arches and tips of transverse processes. Ventral edge of aponeurosis does not touch vertebrae. Anteriorly it is buried within back muscles, but from ninth thoracic back is exposed as broad shining sheet just beneath most superficial aponeurosis of trunk, adjacent to midline, and continuing posteromedial direction of longissimus fibers to insert on summits of neural spines of tenth thoracic and following vertebrae. From its medial side, beginning about level of eighth thoracic, this aponeurosis sends off another, perpendicular to itself, passing ventromedially to insert as separate tendons on metapophyses of posterior thoracics and succeeding vertebrae. (These tendons, however, are nearly inseparable from those of transversospinalis fascicles lying dorsal to them and medial to spinous aponeurosis. Transversospinalis fibers, passing aft from neural spines, insert on dorsal side of metapophysial sheet and possibly even on medial side of spinous sheet. It appears that all fibers lying above metapophysial sheet are transversospinalis, but it must be borne in mind that the latter mass is inseparable from longissimus throughout nearly its whole length, and it is difficult to draw precise boundaries between them.) Some fibers even arise from underside of metapophysial sheet and pass posterolaterally to insert on medial side of main longissimus sheet. Just forward of base of flukes, spinous sheet's ventral edge diverges from fleshy part of muscle, the aponeurosis continuing posteromedially to end of tail. Metapophysial sheet, now separated from other and still buried in muscle, divides into separate round tendons to aftermost caudals.

Slijper (1946, table 3) found the spinous insertions beginning on the 13th thoracic rather than the 10th, and the metapophysial on the 16th, which I was not able to precisely determine, perhaps due to the greater age of my specimen. In his manatee, both insertions began on the sixth thoracic. (Murie does not describe the back muscles in detail.)

Iliocostalis System

Least developed of the epaxial systems; consists of a single unit and has no attachment to pelvis. M. ILIOCOSTALIS THORACIS (IIT: Figures 3, 22–24, 41, 42, 49) [Murie, 1872:144, fig. 8: "cervicalis ascen-

dens" + "sacro-lumbalis"].-Forms long, narrow band, widest (5.5 cm) at level of ninth rib, and less than 1 cm thick; lateral to longissimus and covering ribs just distal to their angles. Consists of series of bundles of fibers pinnate on small tendons, oriented generally anteroventrally. Extends from seventh cervical to last rib, where its after end abuts against forward end of intertransversarius coccygeus. Dorsal edge fused with longissimus from anterior end back to sixth rib. Behind this, aponeurotic sheet covering trunk is connected to rib cage along line separating iliocostalis and longissimus. Slijper (1946:47, 74, table 3) speaks of an "ilio-costalis lumborum," fused with longissimus in the dugong but free in the manatee; neither I nor Murie (1872) observed such a structure. Slijper (1946:74) adds that (in Trichechus but evidently not Dugong) this muscle is also separate from "intertransversarius caudae dorsalis" (my intertransversarius coccygeus), seemingly precluding identity of the latter with his "ilio-costalis lumborum," though in Dugong intertransversarius is indeed tightly adherent to a continuation of abovementioned aponeurosis between longissimus and laterally adjacent muscles. Finally, he (Slijper, 1946:74) states that an "ilio-costalis cervicis" even continues iliocostalis as far as atlas; Murie (1872: 144) found an attachment to the axis, but I saw no insertion forward of seventh cervical.

Origin: Tendinous and fleshy from lateral sides of ribs just distal to angles.

Insertion: Tendons with their pinnate fibers pass anteroventrally, each overlapping ones ahead of it. Tendons narrow as they approach surface of muscle and insert, along with some fibers, on protuberances just distal to muscle's areas of origin on posterolateral sides of ribs, four or five ribs forward of tendons' points of origin. Only a few fibers attach to first rib, just lateral to tuberculum. A tendon inserts on transverse process of seventh cervical, in fusion with longissimus.

DEEPER MUSCLES OF THE NECK

M. RECTUS CAPITIS DORSALIS ?MAJOR (RCMa: Figures 12, 15, 21, 40) [Murie, 1872:145; "rectus capitis posticus major," in part?].—Small, fusiform; 1 cm wide; lies ventral to dorsomedial edge of semispinalis capitis.

Origin: Fleshy from after end of neural spine of

axis. In my specimen it was somewhat asymmetrical, the muscle on left side arising posterior to its fellow, from connective tissue slightly behind spine of axis.

Insertion: Tendinous onto top of supraoccipital, just below nuchal line and adjacent to midline.

M. RECTUS CAPITIS DORSALIS ?INTERMEDIUS (RCI: Figures 12, 15, 21, 38, 40) [Murie, 1872:145: "rectus capitis posticus major," in part?].—Robust; medial to semispinalis capitis just ventral to rectus major.

Origin: Fleshy from apex of axis, anterolateral to rectus major.

Insertion: Fleshy and tendinous onto supraoccipital ventral to rectus major, from midline out to semispinalis capitis, and from near nuchal line down onto exoccipital along posterior border of semispinalis capitis insertion.

M. RECTUS CAPITIS DORSALIS MINOR (RCMi: Figures 12, 15, 21, 36, 37, 39) [Murie, 1872:145: "rectus capitis posticus minor"].—Fused with rectus intermedius, as in manatee.

Origin: Fleshy from apex of atlas, adjacent to midline.

Insertion: Fleshy onto supraoccipital in fusion with rectus intermedius.

M. RECTUS CAPITIS LATERALIS (RL: Figures 6, 13–15, 20, 22–25, 30, 31, 35–37) [Murie, 1872:145, fig. 29: "rectus lateralis"; Murie, 1880:34, pl. 8: fig. 5].—About 4.5 cm long, 1.5 cm wide.

Origin: Fleshy from tip of transverse process of atlas and for about 3 cm anteroventrally along the process.

Insertion: Fleshy on posterolateral side of paroccipital process, with an extension of about 1 cm anteroventrally onto, apparently, proximal end of stylohyoid (as in manatee; perhaps homologous to jugulohyoideus?); also very slight tendinous attachment to most posteroventral edge of squamosal.

Though well developed in the manatee, a rectus capitis ventralis (Murie's "rectus (capitis) anticus minor," 1872:147, fig. 29; 1880:34, pl. 8: fig. 5) was, surprisingly, totally absent in my specimen, which had no muscular connection between the ventral arch of the atlas and the base of the skull. There is a partly separable deep division of the longus capitis arising from cervicals 5 and 6, but this hardly seems a likely homolog.

M. OBLIQUUS CAPITIS CAUDALIS (OCa: Figure 21, 36–40) [Murie, 1872:145: "obliquus inferior"].—Well developed, about 3 cm wide.

Origin: Fleshy from side of neural arch of axis, from edge of apex down to postzygapophysis.

Insertion: Runs steeply anteroventrally and laterally to fleshy insertion on posterolateral side of neural arch of atlas, from within about 2 cm of midline out nearly to tip of transverse process.

M. OBLIQUUS CAPITIS CRANIALIS (OCr: Figures 14, 15, 24, 25, 35, 37) [Murie, 1872:145: "obliquus superior"; Murie, 1880:34, pl. 8: fig. 5].—Very small bundle of fibers ventromedial to rectus capitis lateralis.

Origin: Fleshy from anteroventral side of transverse process of atlas, adjacent to anterior articular surface.

Insertion: Fleshy on posterior side of exoccipital, between condyle and insertion of brachiocephalicus. In manatee attachment seems to be slightly farther outboard and nearer stylohyoid.

M. STERNOMASTOIDEUS (Stm: Figures 6, 13, 14, 22, 23, 34, 35) [Murie, 1872:152, figs. 9, 29, 30; Murie, 1880; pl. 8: fig. 5].—Very long, narrow, fusiform; passes deep to parotid gland together with brachiocephalicus, separated from latter by external jugular vein. Stannius (1845:34), in asserting connection of this muscle with the deltoideus, mistook the cephalohumeralis for the sternomastoideus.

Origin: Fleshy from ventral side of manubrium adjacent to midline; inseparable from sphincter colli profundus pars auris adjoining it behind, and medial to pectoralis major (not anterior as in manatee).

Insertion: By long, narrow tendon onto anteroventrolateral side of posttympanic process of squamosal. Imperfectly divided into two or more bundles, but all insert ultimately on this same tendon; no aponeurosis or other part branching off inner side as in manatee.

M. STERNOTHYROIDEUS (Stt: Figures 5, 23–28, 31, 34, 35, 41) [Owen, 1838:38; Murie, 1872:179, fig. 9].—Broad, thin sheet covering ventral side of trachea, formed by muscles from each side converging dorsal to manubrium and running forward touching in midline. Not divided by any fibrous bands.

Origin: Tendinous from anterior edge of first costal cartilage and anterodistal edge of first rib; covered by sternocostalis.

Insertion: Fleshy on posteroventral side of thyroid cartilage, behind thyrohyoideus.

M. SCALENUS (Sc: Figures 6, 22-25, 35-37, 41, 42)

[Stannius, 1849:36: "scalenus posticus"; Murie, 1872:152, fig. 29; Murie, 1880:35, pl. 8: fig. 5].—Prominent, about 5 cm wide, immediately beneath subscapularis. Serratus magnus arises from dorsal edge. Not in separate bundles as shown by Murie (1880:35), but partly divisible into superficial and deep portions as in manatee.

Origin: Fleshy from first two ribs distal to their angles; in vicinity of third rib becomes indistinguishable from serratus. (Murie [1872, 1880] recorded its attachment to first three ribs.)

Insertion: Fleshy and tendinous on lateral extremities of transverse processes of cervicals 2-4, ventral to longissimus attachments, and on posteroventral side of transverse process of atlas ventral to longissimus and dorsal to longus colli. Murie did not find an atlas insertion in his first manatee (1872), but did in the second (1880); however, I saw no superficial accessory tendon as in the latter instance. Anteriorly muscle is partly covered by shining tendinous sheet, as in manatee.

M. LONGUS CAPITIS (LoCa: Figures 13, 14, 24, 25, 35, 41) [Murie, 1872:147, fig. 29: "rectus (capitis) anticus major"; Murie, 1880:34, pl. 8: fig. 5].—Very prominent and powerfully developed; lies anteromedial and parallel to scalenus and is similar to it in appearance, though slightly smaller.

Origin: Tendinous from anteromedial side of ventral process and ventral side of neck of first rib, and by thin tendinous slip (penetrating longus colli between divisions 1 and 2) from ventral tips of transverse processes of cervicals 5 and 6. Some fibers pass lateral to ventral process of rib and seem to be lost in mass of fasciae and blood vessels in this region. In Murie's (1872) first manatee it arose from undersides of third thoracic vertebra and head of second rib; in his second (1880) it attached to transverse processes of cervicals 5 and 6, centrum of first thoracic, and head of first rib.

Insertion: Fleshy and tendinous on occipitosphenoidal eminence of skull.

M. LONGUS COLLI (LoCo₁₋₃: Figures 25, 35–37, 41) [Murie, 1872:147, fig. 29; Murie, 1880:34, pl. 8: fig. 5].—Imperfectly divided into three parts, as follows, proceeding medially:

—FIRST (LoCo₁: Figure 35).—

Origin: Tendinous from ventrolateral processes of cervicals 5 and 6, lateral to longus capitis origins.

Insertion: Fleshy and tendinous onto ventral side of atlas medial to scalenus.

-SECOND (LoCo2: Figure 35).-

Origin: Tendinous from anterovental side of neck of first rib, anteromedial to longus capitis origin.

Insertion: Runs anteromedially to join with third division on ventral side of atlas, medial to first division.

—тніво (LoCo₃: Figure 35).—

Origin: Broadly tendinous from ventral sides of first and second or third thoracics, and partly from first rib together with second division.

Insertion: Tapers anteriorly and fuses with second division; together they form a single mass, larger than first division, with fleshy and tendinous insertion on atlas between first division and midline. Small tendons of longus colli also insert on ventrolateral sides of cervicals 2–6, just inboard of longus capitis origins.

This arrangement differs in detail from both of those described by Murie (1872, 1880), though the overall pattern is similar. The details of this muscle's attachments are doubtless quite variable, and the same is probably true of many of the muscles in this region, due to the shortness of the neck.

MUSCLES OF THE THORAX

MM. INTERCOSTALES EXTERNI (IntE: Figures 3, 23, 24, 34, 42, 49, 52) [Murie, 1872:151, fig. 9].—Quite strongly developed; run posteroventrally between all ribs, along whole length of each (except caudal edges of distal ends of the most anterior ribs), and covering their anterolateral sides.

I did not observe any distinct levatores costarum, though Murie did (1872:144); the fibers are evidently blended with either the external intercostals or the transversospinalis fascicles.

MM. INTERCOSTALES INTERNI (IntI: Figures 24, 41, 42, 50) [Murie, 1872:151, fig. 44; Murie, 1880, pl. 8: fig. 2].—Considerably thinner than external; run posterodorsally (nearly vertically) between ribs. Do not attach to cartilages.

M. STERNOCOSTALIS (Stc: Figures 22, 23, 24, 35, 41) [Murie, 1880, pl. 8: fig. 2].—Thin, largely tendinous sheet; divided into two slips, the anterior smaller and more tendinous. Murie's (1880) plate also shows a slight division. Seemingly a derivative of the intercostales.

Origin: Tendinous from almost entire lateral

edge of manubrium, anterior to attachment of first rib cartilage.

Insertion: Larger posterior part has fleshy and tendinous insertion on anterolateral sides of distal end of first rib and proximal end of its cartilage; anterior slip diverges to insert farther up shaft of rib.

DIAPHRAGM

The nearly horizontal diaphragm is mostly tendinous, as in *Trichechus*. Its muscular fibers are confined to a narrow band along each side, with fleshy origins from ribs 3–17 near their distal ends and from a transverse line across the rib cartilages and the posterior border of the sternum. The fibers are at most 6–8 cm long and arch dorsomedially and anteriorly. In the manatee the diaphragm extends "from the first to the last rib" (Murie, 1872:154, figs. 44, 49, 50). The high myoglobin content of the diaphragm (Blessing, 1972) suggests its extensive use in hydrostatic adjustments during diving, as well as in respiration.

MUSCLES OF THE ABDOMEN

M. CUTANEUS TRUNCI (CuT: Figures 2, 3, 18, 19, 22, 23, 32, 33, 49, 50–52) [Murie, 1872:163, figs. 8–10, 30, 46, 49, 50: "panniculus carnosus, P.c¹," in part, including "P.c**" and "P.c***"].—Very extensive, mostly thin sheet of loosely connected coarse fibers, extensively veined with fat. Covers underside of body and tail from axilla to base of fluxes, and ventrolateral side of thorax; continuous with its fellow in ventral midline.

Origin: In two parts. Medial part (Murie's "P.c**") arises by fasciae and small tendons from posterolateral edge of sphincter colli profundus pars auris, and is overlapped by latter posteriorly and medially, as described above for that muscle. Between these connections the two muscles are separable along their adjacent borders for about 6 cm. Lateral part arises from fasciae above and behind axilla, widens, and overlaps posterodorsal edge of latissimus. Two parts merge about 12 cm abaft axilla; in fork between them they fuse with diminutive latissimus, ventral to which a few cutaneus fibers pass parallel to it out of axillary fasciae. In this region, bounded by latissimus, cu-

taneus trunci, and (ventrally) pectoralis minor, lies mammary gland (undeveloped in my immature specimen).

Insertion: Lateral fibers sweep back and up onto sides, inserting at dorsal midline by superficial aponeurosis covering back and sides from middle of thorax back to flukes. Anteriorly, fibers end about as high on side as shoulder joint; farther aft, line along which fibers end descends till, at level of anus, muscle is completely on underside of body. More medial fibers run aft in parallel down length of belly and tail nearly to flukes, muscle not decreasing in width behind anus until almost to flukes, where it quickly tapers to a point. This sheet surrounds genital opening and anus, and some fibers attach to hide on side of genital fold just forward of anus. Fibers lateral enough to run aft clear of anus continue parallel for a while, then sweep out and upward to insertion; those near midline behind anus pass posterodorsally in pinnate fashion. Both insert on aponeurosis on muscle's deep side (continuous with aforementioned superficial aponeurosis of back and sides) which attaches to tips of third to about eighth chevron bones in addition to sheathing tail. Lateral border of caudal part of cutaneus, in forward half of tail, forms a fold over this aponeurosis. Thickness of muscle varies greatly as in manatee; from thin (0.5 cm) dorsal and anterior edges it thickens gradually to 2 cm ventrally just ahead of anus, but at level of anus swells very abruptly to about 3.5 cm and then thins again as it runs aft.

This arrangement differs in several respects from that in the manatee. The sheet shown by Murie (1872, fig. 8) passing over the whole shoulder region is here absent, though perhaps represented in part by the upper portion of the cutaneus trunci and by the jugularis and scapularis parts of the platysma. The slip to the humerus (Murie, 1872:163, fig. 9: "P.c*"; Stannius, 1845:35) is also absent. In these respects the dugong is more modified from the primitive ungulate condition than is the manatee. In Trichechus the caudal portion is not so well developed as in Dugong; it ends at the sixth chevron bone. Finally, I observed no distinct slip opposite the genital region, as occurred in Murie's female manatee. (Elsewhere, he (1872:162) homologized this with a levator ani.)

M. OBLIQUUS ABDOMINIS EXTERNUS (OAE: Figures 23, 33-35, 49) [Murie, 1872:155, figs. 8, 9, 30, 44,

50].—Covers approximately the distal thirds of ribs, just beneath cutaneus trunci; between its upper edge and lower edge of iliocostalis are exposed ribs and intercostales externi. Composed of separate pinnate segments attached to each rib and directed posteroventrally, parallel to ribs; segments are 9–15 cm long measured in this direction.

Origin: Pinnately from tendons arising along distal thirds of outer sides of ribs 3-19 (and with weaker tendinous sheet to second rib), thus having a serrate dorsal outline; also fleshy from aponeurosis between rib 19 and lumbar and sacral vertebrae, adjacent to intertransversarius coccygeus.

Insertion: By strong shining aponeurosis to ventral midline, forming part of outer rectus abdominis sheath. Muscular portion of obliquus overlapped by that of cutaneus trunci. Posteriorly it tapers to a point ending opposite ischium, a strong aponeurotic sheet still attaching to muscle's deep side.

Thus, apart from the attachment to the second rib, it does not differ from the arrangement in the manatee.

M. OBLIQUUS ABDOMINIS INTERNUS (OAI: Figures 34, 50, 52) [Murie, 1872:155, fig. 9].—Small, thin, and inconspicuous; fibers about 8 cm long, leading anteroventrally and covering transversus abdominis between ends of ribs and rectus abdominis.

Origin: Fleshy from distal ends of ribs 6-19; Murie found it beginning at third rib.

Insertion: By aponeurosis to ventral midline, fibers not quite reaching edge of rectus abdominis. Aponeurosis divides as usual to form parts of both inner and outer rectus sheaths.

M. TRANSVERSUS ABDOMINIS (TrA: Figures 50-54) [Murie, 1872:154, fig. 9: "transversalis"].—Strong layer about 1.5 cm thick and about 7 cm wide.

Origin: Fleshy from medial sides of ribs 3-19 near distal ends; continued somewhat forward of this by aponeurotic attachment, and posteriorly connected to whole anteroventral side of ilium and part of ischium via aponeurosis between last rib and pelvis, from deep side of which aponeurosis it arises. Muscular portion extends back to pelvis; Murie does not mention such a posterior extension.

Insertion: Fibers pass ventromedially to insert on strong aponeurosis lying against wall of abdominal cavity and forming part of inner rectus sheath. Rectus overlaps ventral edge of transversus by about 2.5 cm.

M. RECTUS ABDOMINIS (RA: Figures 23, 24, 33-35,

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41, 49, 50, 52, 53) [Murie, 1872:155, figs. 9, 37, 46, 50].—Strong, about 8 cm wide and 2 cm thick. Pectorales arise from surface of its forward end. Composition of its aponeurotic sheath same as in terrestrial mammals, except that aponeuroses of obliquus internus are absent abaft rib cage, since obliquus does not extend there; and its outer aponeurosis is of course lacking in the sheath forward, where rectus overlies rib cartilages. Cutaneus trunci very tightly adherent to surface of sheath throughout its length. Rectus extends laterally nearly to free ends of ribs.

Origin: Fleshy from posterolateral edge of sternum and after edge of last (in my specimen the fourth) sternal rib cartilage; laterally sends slips forward to third cartilage and, by a tendinous sheet, first and second cartilages and end of first rib (these forward extensions lying superficial to cartilages).

Insertion: Tapers rather abruptly at pelvis to fleshy insertion on middle of anterolateral side of ischium.

MUSCLES OF THE TAIL

The mm. sacrococcygei dorsales lateralis et medialis (Murie's "levatores caudae externus et internus," 1872:144, figs. 8, 39) are continuations of, and inseparable from, respectively, the longissimus and transversospinalis systems, and have already been described with the epaxial spinal muscles.

"M. INTERTRANSVERSARIUS COCCYGEUS" (Intr: Figures 3, 49, 50, 52, 53) [Murie, 1872:146-147, figs. 8, 39, 44, 50: "lumbo-caudalis"].—Conspicuous, very long, narrow, and fusiform, lying along ends of transverse processes from second lumbar to end of tail, and covered only by cutaneus aponeurosis. Forward end abuts against after end of iliocostalis thoracis, though the two are clearly separate and distinguished by different directions of fibers. Murie (1872, fig. 8), however, shows it below and overlapping iliocostalis. Attachment of cutaneus aponeurosis along dorsal edge of iliocostalis continues along intertransversarius. Latter is, on its deep side, separated by its aponeurosis from short fibers (Intra, Figures 50, 52), divided into dorsal and ventral bundles, lying between transverse processes. The long, fusiform intertransversarius probably developed by fusion of short bundles of this type lying outboard of tips of transverse processes.

Origin: Fleshy from after edge of last rib at

about its middle, from crest on lateral side of proximal end of ilium, and from aponeurosis on its deep side which passes from last rib to lumbar vertebrae and attaches to tips of transverse processes from second lumbar to posterior caudals. Begins in manatee at sacral or first caudal.

Insertion: Aponeurosis from deep side extends laterally onto ventral side of muscle and turns dorsally again, passing into muscle through about the forward two-thirds of its length, and forming an internal tendon of pinnate insertion for fibers passing posteroventrally from lateral surface of deep part of aponeurosis. Farther aft (about middle of tail) this tendon emerges onto ventrolateral side of muscle, and continues back to insert on transverse processes of aftermost caudals. Murie, however, found it only along first 8 or 9 caudals, ending by a tendon on surface of sacrococcygeus ventralis lateralis. Stannius (1845:35-36; 1849:22) describes a system of "Musculi transversarii," with inferior and superior parts, seemingly answering to my intertransversarius at least in part, but evidently passing forward across all the ribs, outboard of the iliocostalis, attaching to each of them!

M. SACROCOCCYGEUS VENTRALIS LATERALIS (SVL: Figures 49–52) [Murie, 1872:145–146, figs. 8, 9, 37, 39, 44, 50: "sacro-coccygeus"].—Broad but rather thin (1.5 cm or less, decreasing posteriorly and ventrally); for most of length triangular in cross-section, intertransversarius lying on its dorsolateral side. Anteriorly on deep side, fuses with sacrococcygeus ventralis medialis. Covered by cutaneus aponeurosis.

Origin: Fleshy from undersides of tips of caudal transverse processes and aponeurosis between them, and anteriorly from medial sides of ribs 17-19 and ventral sides of 16th thoracic and following vertebrae, in fusion with medialis. A long, narrow, fusiform part even extends forward, ventral to diaphragm, to tendinous attachment on sides of keels of thoracics 12 and 13, adjacent to midline, and with possibly some tendinous strands going even beyond. This part, entirely continuous with sacrococcygeus mass, evidently corresponds to the separate quadratus lumborum slips found by Murie (1872:146, fig. 44); these, however, only went as far forward as last two thoracics and last rib. His sacrococcygeus proper also extends only as far as last rib. Stannius (1845:35) found hypaxial muscles extending only about to last lumbar vertebra.

Insertion: Aponeurotic onto tips of second and

following chevron bones and undersides of aftermost caudals, covering medialis. Muscular part extends back about to middle of flukes. Insertion in manatee begins at third chevron bone.

M. SACROCOCCYGEUS VENTRALIS MEDIALIS (SVM: Figure 51) [Murie, 1872:146, figs. 9, 37, 39, 44: "infracoccygeus"].—Lies beneath lateralis; fused with it in sacral and anterior caudal region. Fibers more posteriorly oblique than those of lateralis.

Origin: Fleshy from lateral sides of all chevron bones, fasciae between them, and ventrolateral sides of caudal centra; and from ribs and thoracic and lumbar vertebrae in fusion with lateralis, as described above.

Insertion: By thick aponeurosis (together with lateralis) on tips of second and following chevrons and undersides of aftermost caudals. Aponeurosis not as divided into separate tendons as seems to be the case in the manatee. Covers most of muscle's lateral surface.

"M. FLEXOR HAEMALIS" (FH: Figure 51).—Not found in Murie's manatee; slender, cylindrical, lying along tips of chevron bones, increasing somewhat in size posteriorly, and encased by the rather closely adherent sacrococcygeus ventralis aponeurosis.

Origin: Fleshy and tendinous from tips of seventh and following chevrons.

Insertion: Fibers pass posterodorsally onto externally enveloping tendinous sheet, which continues in this direction and sweeps inward to tips of eighth and following chevrons and ventral sides of aftermost caudals.

MUSCLES OF THE SHOULDER

M. TRAPEZIUS (Trp: Figures 3, 5, 12, 13, 15, 18-20, 22, 43, 44) [Murie, 1872:156, fig. 8].—Rather thin sheet covering nearly entire blade of scapula, superficial to supraspinatus and infraspinatus, and partly covered by partes temporalis and scapularis of platysma.

Origin: By aponeurosis from dorsal midline, anteriorly just reaching skull near lateral end of nuchal line, and extending back to level of caudal angle of scapular cartilage. Aftermost fibers not as posteriorly directed as in manatee, and do not arise as far back on midline. Anteriorly a separate slip 1.5 cm wide arises by a tendon from anterolateral

side of sigmoid ridge of squamosal, dorsal to cephalohumeralis origin; this tendon may be traced up as far as nuchal line, adherent to bone.

Insertion: Tendinous on entire length of scapular spine and along a line diverging thence and crossing infraspinatus at about a 50° angle towards caudal angle of scapular cartilage. This line forms juncture between trapezius above and deltoideus and teres major below, and on it inserts pars scapularis of platysma. Above dorsal end of scapular spine is a tendinous embayment in trapezius, about 4.5 cm long, nearly dividing it into cervical and thoracic portions. Dorsal half of this tendinous band not attached to bone beneath. In Trichechus, trapezius evidently attaches only to scapular spine and not to surface of infraspinatus.

M. RHOMBOIDEUS (Rh: Figures 20, 22, 46, 47) [Murie, 1872:156, figs. 8, 13].—Small and narrow as a whole, though individual loosely connected bundles of fibers are long.

Origin: Aponeurosis in dorsal midline of anterior thoracic region, just beneath trapezius aponeurosis. Fibers begin about 3 cm from midline, just over after corner of splenius.

Insertion: Fleshy on nearly whole vertebral border of scapular cartilage, on its medial side, to within 2 cm of caudal angle. Ventrally it is in contact with serratus and overlaps it by about 1 cm.

M. SERRATUS MAGNUS (SeM: Figures 3, 18–20, 22, 23, 33, 34, 41–43, 46, 47) [Murie, 1872:153, figs. 13, 29].—Divided into anterior (SeM_a) and posterior (SeM_p) parts, latter overlapping and fusing with former near insertion. On medial side change in direction of fibers appears about 6 cm farther aft than on lateral side. The two parts are fully separable only near muscle's attachment to scalenus.

Origin: Anterior part, from dorsomedial edge of scalenus and tendinously from angle of first rib. Posterior part, tendinous and fleshy from second rib about 4 cm distal to its angle and from progressively more distal parts of ribs 3-9; merges ventrally with scalenus and posteriorly with obliquus abdominis externus and intercostales externi. On its inner side its fibers are seen to attach pinnately to tendinous bands from ribs.

Insertion: Fleshy and tendinous onto whole medial side of scapular cartilage and strip about 3 cm wide along vertebral border of scapula. Fibers of anterior part insert on nearly all of this

area; those of posterior part, lying lateral to former, occupy aftermost edge of this area and extend forward thence, ventral to and diverging from main area of insertion, ending about halfway to forward edge of scapula. Insertion of posterior part extends down after edge of scapula to teres major protuberance. Superficial fibers of posterior part insert pinnately on superficial tendinous sheet.

In the manatee, Murie (1872:153) traced the serratus only as far back as the sixth rib, and distinguished a part of it extending to the atlas. I did not observe this, nor the "twist" he described in "the nuchal portion of the muscle". He did not find separate anterior and posterior parts.

M. CEPHALOHUMERALIS (Ch: Figures 5, 13, 19, 22, 23, 33, 34, 46, 47) [Murie, 1872:156, figs. 13, 29: "cephalo-humeral"].—Slender and strap-like, descending steeply across side of neck and covering forward side of shoulder.

Origin: Tendinous from anterolateral side of lower end of sigmoid ridge of squamosal, immediately behind auditory meatus. Murie may be wrong in saying it arose from "outer occipital."

Insertion: Passes ventrally and posteriorly around upper end of humerus, crossing and covering deltoid crest, its inner edge fusing somewhat with brachiocephalicus just medial to deltoid crest. Passes down nearly whole length of front side of humerus, and ends by flat, thin tendon in fascia beneath sphincter colli superficialis and in close association with front edge of pectoralis major, near latter's insertion. Also a partial tendinous insertion onto humerus at upper end of pectoralis major insertion.

M. BRACHIOCEPHALICUS (Brc: Figures 6, 14, 15, 22, 23, 33–35, 46) [Murie, 1872:157, fig. 13: "levator claviculae(?)"].—Slender and strap-like, similar to cephalohumeralis and nearly parallel with and posteromedial to it; passes deep to portion of parotid gland, parallel to sternomastoideus.

Origin: Tendinous from posteroventral edge of paroccipital process of exoccipital, between rectus capitis lateralis and obliquus capitis cranialis.

Insertion: Tendinous into fascia on medial side of deltoid crest of humerus, in fusion with cephalohumeralis.

M. LATISSIMUS DORSI (LaD: Figures 22, 32, 33, 46, 47) [Stannius, 1849:14, 16; Murie, 1872:153, figs. 8, 9, 13; Bahrdt, 1933:237, fig. 22].—Relatively small, partly fused posteriorly with cutaneus trunci. Passes

dorsal to mammary gland. Lies superficial to ribs and intercostales between serratus and obliquus abdominis externus; has no direct connection to ribs, as it evidently does in the manatee.

Origin: Anterior edge and medial side of cutaneus trunci between latter's lateral and medial portions.

Insertion: Pinnate onto flat tendon attached to humerus in fusion with tendon of pectoralis minor (q.v.); not connected to insertion of teres major, in contrast to *Trichechus* and many other mammals.

M. PECTORALIS MAJOR (PMa: Figures 22, 23, 33-35, 46-48) [Murie, 1872:157, figs. 9, 13, 30; Bahrdt, 1933:238, fig. 22].—Wide and strong; 2 cm thick anteriorly.

Origin: Fleshy and tendinous from ventral side of sternum (between sphincter colli profundus pars auris and sternocostalis) from its forward end to within about 2 cm of its after end; and from surface of rectus abdominis for about 3 cm posterolaterad from sternum, out to medial sides of fourth rib cartilage and pectoralis minor insertion. A small fleshy slip also arises from forward edge of distal end of fourth rib cartilage.

Insertion: By strong tendon onto anteromedial side of humerus at lower end of deltoid crest. On dorsal side of muscle a very thin, anteriorly partly separable sheet, more anterior in direction, joins to tendon of latissimus and pectoralis minor. From muscle's distal (posterior) edge a smaller but strong tendon is sent off, nearly perpendicular to rest of muscle, to pass across elbow joint and insert on joint capsule, on proximal end of radius beneath biceps tendon and adherent to brachialis, and possibly on adjacent tip of ulna. (The radial insertion was observed by Murie but not Bahrdt.) Ventrally, a tendinous sheet comes off pectoralis major and crosses brachialis to joint superficial fascia on anterior side of forelimb.

M. PECTORALIS MINOR (PMi: Figures 22, 23, 38-35, 46, 47) [Murie, 1872:157, figs. 9, 13, 30].—Much smaller than pectoralis major, which overlaps and fuses with its forward edge. After part covered only by medial part of cutaneus trunci. Passes medial to mammary gland.

Origin: From surface of rectus abdominis to within 1 cm of latter's lateral border and approaching to within about 3 cm of midline. Anterolaterally adjoins posterior edge of fourth rib cartilage. The trend of its fibers is continued posteromedially by glistening fascia on surface of

rectus abdominis, parallel to obliquus abdominis externus fascia farther aft, and crossing over fascia of obliquus abdominis internus.

Insertion: Pinnate onto flat tendon joining that of latissimus dorsi and attaching to humerus on a line from after side of pectoralis major insertion up ridge (actually medial side of deltoid crest) forming lateral side of bicipital groove. In manatee, inserted onto head of humerus.

In using the terms "pectoralis major" and "pectoralis minor," I am merely following Murie's denotation of the muscles' relative sizes and not taking a position on their homologies with the pectoral muscles of other mammals. The anteriorly directed deep division of the pectoralis major, however, is significant in this connection and seems to be a vestige of a "posterior deep pectoral" sheet.

MUSCLES OF THE FORELIMB

Attention should be called here to the illustrations of the manatee's forelimb provided by Bahrdt (1933, fig. 24), especially the schematic cross-sections.

M. DELTOIDEUS (D: figs. 3, 5, 18–20, 34, 43, 44) [Murie, 1872:158, fig. 8; Bahrdt, 1933:237, fig. 22].—Prominent, up to 1.5 cm thick.

Origin: Fleshy from tip of acromion process and after side of scapular spine, and along tendinous band (in common with trapezius, q.v.) crossing surface of infraspinatus to rear edge of scapula. This band attaches to surface of infraspinatus by a thin tendinous sheet. In manatee, muscle is evidently attached only to scapular spine.

Insertion: Fleshy on deltoid crest of humerus; not divided as in *Trichechus*, nor is there an extension toward elbow. (This extension was evidently not found by Bahrdt in his manatee.) Near insertion, after half of medial side of muscle is covered by shining tendinous sheet on which most of posterior fibers insert pinnately.

M. SUPRASPINATUS (Sup: Figures 5, 19, 20, 34, 43, 44, 46, 47) [Murie, 1872:156, fig. 13].—Quite massive; extends about 3 cm in front of scapula and adheres closely to subscapularis. Upper part crossed by a number of small tendinous bands generally parallel to fibers, but muscle is not complexly pinnate.

Origin: Fleshy from whole supraspinous fossa of scapula.

Insertion: Anterior fibers insert on tendon within muscle which does not extend much above lower

end of scapular spine; this, along with most of fleshy part of muscle, attaches to summit and posterolateral side, and somewhat to medial side, of greater tuberosity of humerus. A partly separable and entirely fleshy division of muscle arises chiefly from lower edge of scapular spine and fuses posteriorly with infraspinatus; its insertion is continuous with that of latter rather than with rest of supraspinatus.

M. INFRASPINATUS (Inf: Figures 20, 43, 44) [Murie, 1872:156, fig. 8].—Considerably smaller than supraspinatus; entirely covered by deltoideus and trapezius. Extends about 3 cm behind scapula. Near insertion, anterior fibers mingle with those of supraspinatus.

Origin: Fleshy from infraspinous fossa of scapula and base of scapular spine, as far down as ventral end of spine.

Insertion: Pinnate on strong tendon (visible on middle of lower part of lateral side) attaching to lateral edge of greater tuberosity of humerus, between head and deltoideus insertion, in fusion with after part of supraspinatus.

M. SUBSCAPULARIS (Su: Figures 43, 46, 47) [Murie, 1872:156, figs. 9, 13].—Covers nearly whole medial side of scapula, extending about 3 cm forward of and abaft scapula (measured just above neck); closely adherent to supraspinatus anteriorly.

Origin: Fleshy from medial side of scapula below serratus insertion, down to 1 cm above border of glenoid cavity. For about 1 cm abaft neck of scapula it arises from aponeurosis between rear edge of scapula and front edge of teres major.

Insertion: Narrows and passes between scapula and coracobrachialis to strong tendinous and fleshy insertion on posteromedial side of lesser tuberosity of humerus. A tendinous sheet covers large part of medial side of muscle; forward of this another tendinous band, about 1 cm wide, thickened posteriorly and buried in muscle anteriorly, is visible; both pass down into humeral insertion, and have fibers inserted pinnately on them.

M. TERES MAJOR (Ter: Figures 3, 18-20, 43, 44, 46, 47) [Stannius, 1849:14; Murie, 1872:156, figs. 8, 13; Bahrdt, 1933:237, fig. 22].—Prominent and well developed.

Origin: Fleshy from posterior edge and lateral side of scapula and its cartilage, from and including tip of teres major process to halfway along edge of cartilage.

Insertion: Pinnate onto strong superficial tendinous sheet attached to posteromedial edge of shaft of humerus. An aponeurosis connects muscle's front edge to rear edge of scapula.

A teres minor is lacking in both dugong and manatee.

M. CORACOBRACHIALIS (Cob: Figures 46, 47) [Barkow, 1851:119; Murie, 1872:159–160, fig. 13: "biceps, B¹"; Murie, 1880:32; Bahrdt, 1933:237, figs. 22, 24: "biceps," in part].—Fusiform; consists of several distinct bundles; complexly pinnate. Lies posterior to lesser tuberosity of humerus and crosses subscapularis and teres major insertions.

Origin: Fleshy from medial side of coracoid process of scapula.

Insertion: Tendinous on proximal side of medial epicondyle of humerus.

M. BICEPS BRACHII (B: Figures 44, 46–48) [Barkow, 1851:119; Murie, 1872:159–160, fig. 13: "biceps, B2"; Murie, 1880:32, pl. 8: fig. 3; Bahrdt, 1933:237, figs. 22, 24: "biceps," in part].—Fusiform; single-headed. Smaller than coracobrachialis. Fills bicipital groove of humerus and crosses latissimus and pectoralis insertions. Bahrdt thought it more strongly developed in *Dugong* than in *Trichechus*.

Origin: Fleshy from anterolateral rim of glenoid cavity.

Insertion: Pinnate on strong externally sheathing tendon to coronoid process of ulna and adjacent medial side of neck of radius, covering distal insertion of pectoralis major just behind proximal insertion of brachialis.

M. TRICEPS BRACHII [Murie, 1872:158, fig. 13: "triceps"; Murie, 1880, pl. 8: fig. 3; Bahrdt, 1933:236, figs. 22, 24: "triceps"].—Very massive, with three divisions.

—LONG HEAD (TrLo: Figures 43, 44, 46–48) [Bahrdt, 1933:236: "third" head].—Largest division; thick and fleshy.

Origin: Fleshy, and pinnate from superficial tendon, from after edge of neck of scapula, for 3 cm dorsally from glenoid cavity.

Insertion: Pinnate on deep tendon onto tip and medial side of olecranon process.

—LATERAL HEAD (TrLa: Figures 43, 44, 47), [Bahrdt, 1933:236: "second" head].—Rather flat; fused distally with medial head and anteriorly (less intimately) with brachialis. Partly overlies medial head. Pinnate similarly to long head.

Origin: Tendinous and fleshy from after side of neck of humerus.

Insertion: On olecranon process, lateral and partially deep to insertion of long head, by a shining tendinous sheet covering lateral side of olecranon and continuous with antebrachial fascia. Also has fleshy attachment to olecranon by way of fusion with medial head.

—MEDIAL HEAD (TrM: Figures 44, 46, 47): [Bahrdt, 1933:236: "first" head].—Slightly larger than lateral head; thin laterally where latter overlies it, but much thicker medially, where it contains a tendon.

Origin: Fleshy from posterior side of humerus, from neck down onto after side of medial epicondyle.

Insertion: Fleshy, and pinnately on tendon, onto olecranon process, lateral, anterior, and medial sides.

As in the manatee, no separate anconeus was observed; it may have become fused with the triceps.

M. BRACHIALIS (Br: Figures 43, 44, 46–48) [Barkow, .1851:119: "brachialis internus"; Murie, 1872:160, figs. 8, 13: "brachialis anticus"; Murie, 1880:32, pl. 8: fig. 3; Bahrdt, 1933:237, figs. 22, 24].—Very strongly developed. Posterior border fused with and overlapped by lateral head of triceps. Distally has two divisions, and is fused with brachioradialis at latter's origin. Passing down radius, it is partly covered by shining fascia.

Origin: Fleshy from whole lateral side of humerus, from neck down to lateral epicondyle. Some fibers from superficial shining fascia.

Insertion: First, fleshy and tendinous of radial tuberosity; second, tendinous along line crossing anterior side of radius mediodistally, finally ending tendinously on anteromedial side of distal end of radius, adjacent to brachioradialis. Part of its tendon passes into wrist fasciae beneath abductor pollicis longus and flexor carpi radialis. Fibers pinnate on the various tendons.

Barkow does not mention a separate proximal insertion, nor does Bahrdt; Murie (1872:160) found the insertion on "the upper half of the radius." Bahrdt's distal insertion was "fleshy," and he did not find an extension beyond the radius (though I found this of almost negligible extent).

M. BRACHIORADIALIS (Brr: "Figures 43-47) [Murie, 1872:158, fig. 8: "supinator longus"; Bahrdt,

1933:238, figs. 22, 23, 24].—Forms anterior edge of forearm.

Origin: Fleshy and by single strong tendon from anterior side of lateral epicondyle of humerus, continuous with origins of brachialis and extensor carpi radialis. Some superficial fibers arise from underside of a shining fascia covering brachialis and brachioradialis near elbow joint.

Insertion: Pinnate on central tendon which becomes exposed at distal end of radius and covers latter's anterior side; inserts on lateral sides of anteriormost carpals, with its anterior edge prolonged down to forward side of proximal end of metacarpal I.

Neither Bahrdt nor Murie noted a fusion with the brachialis or an extension to the metacarpal, but the relations of the muscle are such that these are to be expected.

M. EXTENSOR CARPI RADIALIS (ECR: Figures 43-45) [Murie, 1872:158, fig. 8; Bahrdt, 1933:238-239, figs. 22, 23, 24].— Not subdivided. Quite wide (1.7 cm) proximally.

Origin: Fleshy and tendinous from anterolateral side of lateral epicondyle of humerus, between origins of brachioradialis and extensor digitorum communis.

Insertion: Complexly pinnate onto tendon passing beneath abductor pollicis longus and extensor pollicis brevis et longus, and through anterior groove in distal end of radius, to proximal end of metacarpal II. No connection to metacarpal III as in Bahrdt's and Murie's specimens. Murie found its tendon of insertion crossed by those of "primi internodii pollicis" (part of my extensor pollicis) and "long supinator" (my brachioradialis); but since latter inserted on anterior carpal, just as in dugong, it would seem unable to cross extensor carpi radialis; so his statement is evidently in error. Indeed, Murie's (1872) figure 8 shows the two muscles lying parallel. He probably meant that extensor pollicis crosses brachioradialis and extensor carpi radialis.

M. EXTENSOR DIGITORUM COMMUNIS (EDC: Figures 43–45) [Murie, 1872:159, fig. 8; Bahrdt, 1933:239, figs. 22, 24].—Very narrow proximally and much less prominent than adjacent muscles; widens distally.

Origin: Tendinous from lateral epicondyle of humerus behind extensor carpi radialis, and from elbow joint capsule; fleshy and tendinous from lateral side of proximal end of radius.

Insertion: Complexly pinnate. Passing through anterior groove on ulna, adjacent to extensor pollicis, its tendon divides over distal carpals into three parts, passing respectively to second phalanges of digits II and III and to proximal phalanx of IV; no branch to v as in Murie's and Bahrdt's animals. Tendon to IV comes off higher than others.

M. EXTENSOR DIGITI QUINTI (EDQ: Figures 48-45) [Murie, 1872:159, fig. 8: "extensor minimi digiti"; Bahrdt, 1933:239, figs. 22, 24].—Closely adherent deeply to extensor digitorum communis.

Origin: Tendinous from lateral epicondyle of humerus behind extensor digitorum communis, from joint capsule, posterolateral corner of proximal end of radius, and lateral corner of semilunar notch of ulna.

Insertion: Pinnate on both sides of tendon passing through posterior groove in ulna and diverging from that of extensor digitorum communis; inserts on proximal end of metacarpal v and also continues down to insert on proximal phalanx. Tendon's division lies over proximal end of metacarpal; branch to metacarpal is so short that it hardly constitutes a separate tendon.

M. EXTENSOR CARPI ULNARIS (ECU: Figures 43, 44) [Murie, 1872:159, fig. 8; Bahrdt, 1933:239, figs. 22, 24].—Flat and smaller than extensor digiti quinti. Proximally overlies extensor pollicis; distally, the bare ulna. Pinnate between deep proximal and superficial distal tendinous sheets.

Origin: By very broad tendon from lateral epicondyle of humerus behind forward half of extensor digiti quinti tendon, and crossing and covering latter's after half. Also, from smaller tendinous attachment on lateral side of olecranon process, beneath triceps tendon and superficial to extensor digiti quinti. Bahrdt describes a bifurcate tendon, but fails to state whether after branch connects to ulna.

Insertion: Becomes tendinous and passes into thick tendinous covering at rear of wrist along with flexor carpi ulnaris. Inserts on posterior sides of aftermost carpal (corresponding to pisiforme) and of proximal end of metacarpal v. Murie found it inserting on unciforme (hamate), os magnum (capitate) and metacarpal. In stating that "its fibers . . . mingle with those of the carpi radialis," Murie

(1872:159) perhaps meant instead the flexor carpi ulnaris.

M. EXTENSOR POLLICIS BREVIS ET LONGUS (EP: Figures 43–45) [Murie, 1872:159, fig. 8: "extensores primi and secundi internodii pollicis"; Bahrdt 1933:240, fig. 23].—Thin and flat; anterior edge overlaps abductor pollicis longus. Almost entirely covered by other extensors. Murie found it partly divisible.

Origin: Fleshy from anterolateral side of shaft of ulna and lateral side of olecranon process.

Insertion: Fibers insert pinnately on tendinous sheet, covering muscle superficially, which passes into tendon, adjacent and subparallel to that of abductor pollicis longus, and emerging from beneath extensor digitorum communis at wrist joint. This tendon passes through posterior groove on radius and inserts on anterolateral side of proximal end of metacarpal I.

?M. ABDUCTOR POLLICIS LONGUS (AbP: Figures 48–47).—My identifications of this and the previous muscle are somewhat uncertain, since their homologs in other animals vary a good deal in attachments and even in presence or absence, and since no other author seems to have described this muscle in a sirenian. I found it well developed, filling the interosseous space laterally.

Origin: Fleshy from posterolateral side of radius and anterolateral side of ulna.

Insertion: Emerges from beneath extensor digitorum communis just proximal to extensor pollicis, and becomes tendinous on deep side where it crosses extensor carpi radialis (which also becomes superficially tendinous at this point); passes obliquely medially across front edge of wrist and onto palm, where it becomes continuous with superficial aponeurosis crossing palm to base of metacarpal v; but chief insertion is onto palmar side of proximal end of metacarpal I.

M. PRONATOR TERES (PrT: Figures 46, 47) [Murie, 1872:160, fig. 13: "pronator radii teres"; Murie, 1880:32, pl. 8: fig. 3; Bahrdt, 1933:240, figs. 22, 24].—Vestigial; represented only by a very thin tendon with few or no fibers of its own, and adherent to antebrachial aponeurosis.

Origin: Anterior side of medial epicondyle of humerus, in fusion with flexor carpi radialis.

Insertion: Medial side of radius, about two-thirds of way down. Quite separable from flexor carpi

radialis except at origin, but adherent to brachialis near insertion.

Bahrdt apparently found it better developed, and it was still more so in Murie's (1872) first manatee, where it had a distinct belly; but in his later dissection it was inseparable from the flexor carpi radialis.

M. FLEXOR CARPI RADIALIS (FCR: Figures 46–48) [Murie, 1872:160, fig. 13; Murie, 1880:32, pl. 8: fig. 3; Bahrdt, 1933:240, figs. 22, 24].—Slightly overlaps and fused posteriorly with flexor digitorum superficialis at origin. Covered by tendinous sheath except near origin; complexly pinnate.

Origin: Fleshy from anterodistal side of medial epicondyle of humerus with pronator teres and flexor digitorum superficialis; fleshy from medial side of middle quarter of shaft of radius.

Insertion: By very wide, strong tendon onto medial side of distal carpal at bases of metacarpals 1 and 11. Murie (1872, 1880) found it attached to bases of metacarpals 1 and 11.

M. FLEXOR DIGITORUM SUPERFICIALIS (FDS: Figures 46, 47) [Murie, 1872:160, fig. 13: "flexor sublimis"; Murie, 1880:32–33, pl. 8: figs. 3, 4; Bahrdt, 1933, figs. 22, 24].—Tendon traceable on surface nearly to origin; on deep side it begins about middle of forearm, and fibers extend nearly to wrist.

Origin: Fleshy from distal side of medial epicondyle of humerus in fusion with flexor carpi radialis and flexor carpi ulnaris; along its after edge it arises from anterior edge of flexor carpi ulnaris, and a few fibers also arise from middle of after side of radius.

Insertion: Pinnate on strong tendon which divides over bases of metacarpals, small posterior part going to join tendon of flexor digitorum profundus to digit III, while larger part inserts on phalanges of digit II. Between these, a very delicate tendon goes to distal part of metacarpal III.

Murie (1872, 1880) found this muscle only partly distinct from flexores profundus and longus pollicis, and inserting on digits 11-1v.

M. FLEXOR DIGITORUM PROFUNDUS (FDP: Figures 43–48) [Murie, 1872:160, fig. 13: "flexor profundus"; Murie, 1880:32–33, pl. 8: figs. 3, 4; Bahrdt, 1933, figs. 22, 24].—Much larger than flexor superficialis. Antebrachial fascia passes between it and flexor carpi ulnaris to insert on posterior edge of ulna. Belly nearly covered by flexores superficialis and carpi ulnaris.

Origin: Fleshy from posterior edge of olecranon process and nearly whole medial side of ulna, encircling part of insertion of long head of triceps.

Insertion: Pinnate on strong tendon which divides below wrist, small posterior part going to phalanges of digit IV, larger, joined by branch of flexor superficialis tendon, to those of digit III.

No flexor pollicis longus is present, which is to be expected from the reduction of the pollex. Murie suggested (1880:33) it might be represented by the tendon from the flexor digitorum mass to the second digit.

M. FLEXOR CARPI ULNARIS (FCU, Figures 43, 45-47) [Murie, 1872:160, figs. 13, 14; Murie, 1880:32-33, pl. 8: fig. 3; Leboucq, 1889:608; Bahrdt, 1933:240, figs. 22, 24].—Evidently fused with palmaris longus.

Origin: Fleshy and tendinous from posterodistal side of medial epicondyle of humerus. Partly divisible; more anterior and superficial part consists of a round, thick tendon, at first barely exposed on surface but spreading out distally into a sheet, thicker forward where covered by posterior edge of flexor digitorum superficialis. Fibers arise from deep side of this sheet. After, more thick and fleshy part passes somewhat anteriorly beneath first, separated from it by ulnar nerves.

Insertion: Deeper part merges with flexor digitorum superficialis, its fibers inserting on latter's internal tendon. Superficial part, though also fused proximally with flexor superficialis, diverges from it, becomes thicker, broad, and flat, widening wrist; and finally attaches tendinously on posteromedial side of proximal end of metacarpal v. Leboucq stated that in a dugong fetus the "muscle cubital interne" inserted tendinously on a tubercle representing the pisiforme.

M. PALMARIS LONGUS (PaL: Figures 43, 45–47) [Murie, 1872:160, figs. 13, 14; Murie, 1880:32–33, pl. 8: fig. 3; Bahrdt, 1933:240, figs. 22, 24].— Inseparable from flexor carpi ulnaris (q.v.), or perhaps absent entirely. In his first dissection Murie (1872, fig. 13) found it parallel to flexor carpi ulnaris, with essentially the same attachments, and apparently with two divisions. He (1872:160) said it "enwraps the [flexor carpi] ulnaris, and is in continuity with the tough superficial fascia of the forearm." In his second dissection (1880) he found a muscle passing from the distal ulna to metacarpal v, which he thought either a palmaris longus or a

"flexor brevis minimi digiti"; and if the latter, palmaris was fused with flexor carpi ulnaris. Bahrdt took both to be represented by a single mass. Freund (1904:390-391) surmised that they should insert farther down on the metacarpal in the dugong than in the manatee, but with only Murie's figures for comparison I can see no difference.

?M. ABDUCTOR DIGITI QUINTI (AbD: Figures 43, 46, 47) [Murie: 1872:161, figs. 13, 14: "abductor minimi digiti"; Murie, 1880:34, pl. 8: figs. 3, 4].—Small bundle, hardly separable from flexor digiti quinti brevis, on posterior and slightly palmar side of metacarpal v.

Origin: Tendinous from antebrachial fascia and palmar side of ulnar carpal.

Insertion: Fleshy and tendinous on posteromedial edge of distal end of metacarpal v.

?M. FLEXOR DIGITI QUINTI BREVIS (FDQ: Figures 46, 47) [Murie; 1872:161, figs. 13, 14: "flexor brevis minimi digiti"; Murie, 1880:33, 34, pl. 8: fig. 3].—Broad, flat mass of fibers without any clear division, though posterior fibers have more posterior direction than others.

Origin: Forms posterodistal continuation of palmar aponeurosis, and thereby has some tendinous attachment to palmar side of ulnar carpal.

Insertion: Fleshy on palmar side of distal end of metacarpal v.

I have arbitrarily followed Murie's 1872 figures in assigning the above two names (his text has their order reversed), though the homologies are hardly certain. Part of the second may correspond to the "opponens minimi digiti" of his second animal (1880:34, pl. 8: figs. 3, 4). It somewhat resembles a palmaris brevis, except for its insertion onto the bone.

The muscles of the palm differed considerably from those Murie described:

MM. LUMBRICALES (Lu III-v: Figures 43, 44, 46-48).—Murie distinguished but a single lumbrical muscle in one animal (1880:33, pl. 8: fig. 4), but it is possible that some of his "superficial interossei" represent the lumbricales of my interpretation. I found three well-developed and distinct muscles, pinnate between superficial proximal and deep distal tendons, attaching to the three posterior digits:

—III (Lu III: Figures 46–48).—The smallest, a flat band.

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Origin: Fleshy from fascia over insertion of flexor carpi radialis tendon.

Insertion: Narrows quickly to tendon inserting on anterior edge of metacarpal III distal to its midsection.

—IV (Lu IV: Figures 47, 48).—Robust and triangular in distal cross-section, extending deeply between metacarpals III and IV.

Origin: Tendinous from wrist fascia beneath tendon of flexor carpi radialis.

Insertion: Tendinous on anterior edge of distal end of metacarpal IV.

—v (Lu v: Figures 43, 44, 46–48).—Robust but flattened.

Origin: Tendinous from wrist fascia behind and adjacent to IV.

Insertion: Fleshy on whole anterior edge of metacarpal v except promixal end.

MM. INTEROSSEI (Into II—IV: Figures 43, 46, 47, 48) [Murie, 1872:161, figs. 13, 14, 15; Murie, 1880:33, pl. 8: figs. 3, 4].—I did not find these in two distinct layers as did Murie, unless his "superficial interossei" are my lumbricales. However, both dorsal and palmar interossei may be represented in the single layer observed, the dorsals having migrated palmad. All seem to be pinnate. I list them by the digits on which they insert:

—II (Into II: Figures 47, 48).—Three hardly separable bundles lie on palmar side of metacarpal. Anterior has fleshy origin from whole after edge of metacarpal I and tendinous insertion on anteromedial side of distal end of metacarpal II. Other two arise tendinously from base and fleshily from palmar side of metacarpal II and insert tendinously at metacarpal-phalangeal joint. Former two may correspond to first interossei dorsales, and latter to first palmar.

—III (Into III: Figures 47, 48).—Imperfectly divisible into forward and after parts, with forward again subdivided. Arises like foregoing from base and palmar side of metacarpal and inserts at metacarpal—phalangeal joint. May represent fused second and third dorsales.

—IV (Into IV: Figures 43, 47, 48).—Partly divisible, after part wider and more noticeably pinnate on surface. Forward part tendinous distally where obliquely crossed by flexor profundus tendon. Origin, as before, tendinous from base and fleshy from side of metacarpal IV, and tendinous insertion on metacarpal-phalangeal joint. Forward part may

be second palmar, after and larger section, fourth dorsales.

The third palmar of human anatomy, attached to digit v, is absent or fused with lumbricalis v, though Murie (1872, 1880) seems to have distinguished it in the manatee. For the interossei as a whole, he described a much more complex arrangement than I encountered, so that it would be pointless to attempt a detailed comparison.

In one manatee Murie (1880:34, pl. 8: figs. 3, 4) found a thumb muscle ("flexor brevis pollicis or . . . adductor pollicis"), but this was absent in my dugong.

MUSCLES OF THE PELVIC AND GENITAL REGIONS

There is no coccygeus muscle, but the strong aponeurosis extending between the whole length of the innominate and the transverse processes of the anterior caudal vertebrae, and continuing aft between the intertransversarius and sacrococcygeus ventralis lateralis, may in part represent the coccygeus.

M. RETRACTOR ISCHII (ReI: Figures 52-54) [Stannius, 1845:9; Stannius, 1849:35: "retractor ischi" or "ischio-caudalis"; Murie, 1872:161-162, figs. 46, 50: ?"ischio- or ilio-coccygeus," in part].—Murie quotes Rapp (1837) by mistake instead of Stannius (1849), concerning this muscle.

I found this muscle fairly thick, though it was thin and weak in Stannius' (1849) specimen; Riha (1911:415) failed to find it at all in his dugong material.

Origin: Fleshy from ventromedial edge of ischium and distal end of ilium.

Insertion: Runs medially and posteroventrally parallel to pelvis to tendinous insertion on side of tip of third chevron bone. In Stannius' (1849) manatee it attached to the first two chevron bones.

I did not observe anything resembling Murie's (1872:162, fig. 50) "levator ani" or "transversus perinaei."

M. ISCHIOCOCCYCEUS (ISC: Figures 49, 52, 53) [Murie, 1872:161–162, figs. 46, 50: "ischio- or iliococcygeus"].—I found this much more completely fused with cutaneus than did Murie, being inseparable from it except at origin. A small slip medial to ischium connects ischiococcygeus with retractor ischii.

Origin: Fleshy from after side of distal end of ischium.

Insertion: Passes aft and fuses immediately with overlying cutaneus. Medial side sheathed by aponeurosis attached to tips of third and following chevron bones, as described with cutaneus; anteriorly aponeurosis also reaches retractor ischii.

M. SPHINCTER ANI (SpA: Figures 49, 50, 52) [Stannius, 1849:41; Murie, 1872:162, figs. 37, 50; Riha, 1911, fig. 14; Freund, 1930:439, figs. 6-8].—Only a single layer of striated fibers, about 3 cm wide, could be discerned external to longitudinal smooth fibers of rectum. Posterodorsal edge in contact with anteroventral end of third chevron bone. Overlain posterolaterally and laterally by cutaneus. Murie is vague as to whether sphincter was distinctly divided into inner and outer parts in the manatee, but it seems not to have been. Riha and Freund indicate an undifferentiated sphincter ani. Stannius found the sphincter ani double.

M. CONSTRICTOR VULVAE (CoVu: Figures 49, 50, 52) [Murie, 1872:162, fig. 50: "sphincter vaginae"; Freund, 1930:438, figs. 6–8].—Band of fibers about 2 cm wide, with both middorsal and midventral fibrous raphes, former attaching to constrictor vestibuli (q.v.). Posterodorsal edge in contact with sphincter ani. Arrangement similar in manatee, as described by Freund.

M. URETHRALIS (U: Figures 52, 53) [Freund, 1930: 438–439, figs. 7, 8].—Thin band about 2 cm wide.

Origin: Tendinous from anterior side of ischium, medial and anteroventral to rectus abdominis attachment.

Insertion: Passes around front of vagina and urethra to join its fellow ventral to peritoneum.

This was not noted by Murie, unless it corresponds to part of his "erector clitoridis," which I doubt. Freund found it in his manatee, where it seemed to have essentially the same relations as in the dugong.

M. CONSTRICTOR VESTIBULI (CoVe: Figures 49, 50, 52-54) [Murie, 1872:162-163, fig. 50: "erector clitoridis"; Freund, 1930:438, figs. 6, 7, 8].— Freund regards the true erector clitoridis, or ischiocavernosus, as absent in the manatee; I provisionally follow his interpretation.

Consists in dugong of two fusiform slips, nearly equal in diameter, tightly united in tendinous wrapper; medial slip much the shorter, its fibers not reaching pelvis.

Origin: Lateral slip, fleshy from medial, and partly lateral, side of distal end of ischium.

Insertion: Becomes encased in thick fibrous covering and inserts into fibrous tissue on dorsal side of vagina, directly above clitoris, anterior to constrictor vulvae and united to latter's middorsal fibrous raphe.

This arrangement seems to correspond more to Murie's specimen than to Freund's, where the two slips of the muscle seem larger and better developed; they are not encased in a tendinous wrapper, and both attach to the pelvis.

The genital muscles of the male dugong have been best described by Riha (1911:413-415), and those of both dugong and manatee by Petit (1925: 251-269); a brief description of the male manatee is given by Murie (1872:163, fig. 37).

Functional Anatomy

I have deliberately refrained from including with the muscle descriptions, in the usual fashion, comments on their "action," for two reasons: first, the "actions" of most of them are obvious from their forms and attachments, though their real functions in the living animal may be very difficult to determine; and second, those on whose functions I wish to comment seem more effectively dealt with as systems than as isolated units. However, a thorough analysis of functional myology is beyond the scope of this paper, which I intend primarily as a descriptive foundation for future analytical work; hence the following comments are only my superficial impressions of the workings of some parts of the animal.

FACIAL MUSCLES

The well-developed platysma complex has two noteworthy features: the curious pars scapularis and the pair of auriculares. For the former I can see no clear purpose, but for the latter several possibilities occurred to me. They may, by pulling the auditory canal against the small auricular cartilage, close it against water pressure during dives; dugongs are said to dive as deep as 10 or 12 fathoms (Annandale, 1905:242). Pinnipeds are able to close the ear canal voluntarily with auricular muscles (Møhl, 1968:175–176), or the muscles may alter the direc-

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tion of the outer part of the canal to improve directionality of hearing; manatees are known to be very efficient at localizing noises (Hartman, 1971:219). Or they may merely be vestigial structures. Yet another explanation is furnished by Fraser and Purves (1960:131–132) in their study of hearing in cetaceans, where they conclude that auricular muscles provide directional hearing by constricting the canals to equalize sound intensities at the cochleae, and may also protect the ears against high sound intensities.

Anyone observing a living sea cow will be impressed by the virtuosity of its facial equipment in feeding (all the more noticeable because this is likely to be the only part of the animal in motion). While I cannot venture here to analyze the dynamics of the dugong's complex lip movements, attention should be called to some of the underlying structural equipment.

As is well known, the sides of the upper lip are controlled separately; their corners are equipped with large stiff bristles and they act together rather like forceps to pull food into the mouth. The substance of the snout is a mass of muscle fibers scattered through dense fibrous tissue, to which are connected three pairs of muscles which act in concert to raise, lower, and pull laterally the corners of the lip. These are arranged in layers on the side of the rostrum: the most superficial (levator nasolabialis) is anteroventral in fiber direction; the middle (maxillonasolabialis), horizontal; and the deepest (lateralis nasi), anterodorsal. The mentalis appears to assist in pulling food into the mouth by raising the side of the lower lip (also armed with bristles). The modification of the lateralis nasi as a snout and lip muscle is noteworthy.

I am at a loss to understand the purpose of the queer triradiate arrangement of the mandibularis, depressor anguli oris, and sphincter colli profundus pars palpebralis; perhaps their lack of attachment to the corner of the mouth is exceptional in this individual, but that would hardly speak for the functional importance of such a connection where it did occur. The mandibularis, combined with the vestigial and mostly tendinous depressor anguli oris, may pull the front of the lower lip transversely, but the function of the palpebralis is not obvious.

The other mouth muscles (orbicularis oris, buccinatorius, retractor labiorum) show nothing un-

usual functionally, though the homology of the latter is unclear.

Without personally verifying Murie's (1872) description of the manatee's facial muscles, I would not venture a functional comparison with the dugong; but the two are basically similar in structure. They also share the remarkable development of blood-vessel bundles issuing from the infraorbital and mental foramina to supply the lip muscles, as well as the general wealth of retia mirabilia throughout the body. These no doubt serve a variety of functions, but the facial plexuses likely provide oxygen reservoirs for the vigorous activity of the lips while submerged. The chewing muscles of the manatee also have a relatively high myoglobin content (Blessing, 1972).

The sphincter colli profundus pars auris is discussed under "Swimming Muscles."

JAW MUSCLES

Without quantitative data, such as muscle weights, on the relative forces exerted by the jaw muscles, a vector analysis of jaw mechanics cannot be given. A qualitative examination of the structures, however, indicates that the dugong has quite a normal sort of "ungulate-grinding" jaw apparatus (to use Turnbull's (1970) term), emphasizing horizontal rather than orthal motion. (That chewing in Dugong is mainly lateral is confirmed by the transverse striations visible on the teeth of many specimens.)

Herring (1972) has given an enlightening account of jaw mechanics in pigs and peccaries that reveals a number of striking similarities between the former and sea cows. The two groups have in common a relatively unrestricted craniomandibular joint lying well above the tooth row, a posteriorly thickened joint capsule, a fairly well-developed coronoid process, a single-bellied digastricus with a lowered origin (on a paroccipital process or the hyoid arch), a massive pterygoid process, highly pinnate adductor musculature, and, of course, lateral chewing; all in contrast to peccaries. The thickened pad behind the mandibular condyle, at least in Dugong, fills the space between the condyle and the postglenoid process, bracing the condyle when it serves as a fulcrum in lateral chewing. The pad may function analogously in pigs, although these lack a

postglenoid process entirely. The elevation of the joint above the occlusal plane is common to many mammals which use the masseter-pterygoid complex extensively for grinding. In both sirenians and pigs, the lowering of the digastricus increases its mechanical advantage for jaw-opening and improves its position for retracting the mandible, but its shortening permits only a small gape. The heavy pterygoid processes probably reflect use of the pterygoidei externi as protractors of the mandible, in sirenians, for use of the rostrum in feeding. Herring (1972:504) suggests that Sus also protracts the mandible for incision. In the adductor muscles, there is a strong resemblance between the patterns of internal tendons of the masseteres in Dugong (Figure 7) and Sus (Herring, 1972, fig. 5D). These morphological and functional similarities suggest that detailed investigation of suoid jaw mechanics should shed light on feeding adaptations in sirenians.

In the light of Herring's discussion, I propose the following as a hypothetical description of the dugong's jaw movements: To use the rostral pads, the jaw is brought forward by the pterygoidei externi and masseteres, and depressed by the digastrici and possibly the geniohyoidei; then closed by the masseteres (superficial division?) and pterygoidei interni, pressure being maintained between the rostral pads. To switch to chewing with the molars, the digastrici retract the mandible and the temporales and zygomaticomandibulares, together with the masseteres (deep division?) and pterygoidei interni, provide the orthal force needed. Most mastication is accomplished by a combination of this orthal force with lateral grinding. The grinding takes place on one side of the mouth at a time, the condyle on that side remaining relatively fixed as the center of rotation of the mandible, while the masseter and pterygoideus internus on that side and the temporalis and zygomaticomandibularis on the other close and draw the jaw medially, grinding the food between the lingual sides of the upper teeth and the labial sides of the lowers, as the latter move dorsomedially. The recovery stroke is made by the pterygoideus externus opposite the fixed condyle.

The jaw apparatus of the manatee differs from that of the dugong chiefly in having the coronoid process extended horizontally quite far forward, providing a better lever arm for the temporalis and zygomaticomandibularis. This increase in orthal strength is evidently correlated with the longer dental series and greater surface area for chewing.

SWIMMING MUSCLES

The sirenian vertebral column does not show any distinct anticliny, nor are distinct diaphragmatic vertebrae present. As in cetaceans, the main point of flexion of the column in swimming is near the level of the anus (Hartman, 1971:118). The undesirability of a flexible thorax in a cetacean or sirenian evidently led to loss of the ancestral transversospinalis structure (prediaphragmatic origin and postdiaphragmatic insertion of spinalis and semispinalis fascicles), and loss of the hind limbs allowed fusion of the transversospinalis with the sacrococcygeus dorsalis medialis, in effect extending the latter up to the anterior thorax. This unit then fused with the larger longissimus system to form a single epaxial extensor mass which, since the thorax was relatively inflexible, bent the spine at the base of the tail and farther aft rather than in the trunk region.

In sirenians, the metapophyses are relatively low on the neural arches and the spines have a slight caudal inclination. Slijper (1946:112-114) notes that in this regard the dugong resembles some, generally more primitive, whales; in other (generally more advanced) whales, the spines of the lumbar and caudal vertebrae incline forward and the metapophyses shift upward. He (1946:112) attributes the latter facts to an increase in importance of the longissimus at the expense of the transversospinalis, "in consequence of the appearance of a more localised mobility." The manatee, on the contrary, has shorter neural spines, larger metapophyses, and longer centra than the dugong, and in these respects tends to resemble the archaeocete whale Basilosaurus. Indeed, Slijper (1946, tables 3, 6) affirms that the transversospinalis is better developed relative to the longissimus in the manatee than in the dugong.

That sirenians are considerably less specialized for swimming than modern cetaceans is additionally clear from such features as lesser streamlining, lower aspect ratio of flukes, very slight development of longissimus and sacrococcygeus ventralis tendons, and absence of a separate system of "fluke elevator" tendons. The latter deficiency implies the

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absence in sirenians of a "double lever" action of the flukes (Parry, 1949), and this is confirmed, at least for manatees, by Hartman's (1971, fig. 17a) observations showing that there is little or no rearward force exerted by the caudal fin during the latter half of a power stroke. Hartman (1971:118) does, however, mention a slight passive lag of the tail behind thrusts of its base.

There are other indications besides the difference in structure of vertebrae and back muscles that manatees are less efficient swimmers than dugongs: the aspect ratio of the caudal fin is still lower, a whale-like peduncle is not developed, the hypaxial muscles do not arise as far forward, the intertransversarius coccygeus does not extend so far forward or back (implying less transverse flexibility and hence agility), and the skeleton is much heavier. Such a difference in swimming ability is consistent with the dugong's open-coast habitat, supposedly more migratory habits, and greater exposure to sharks and killer whales (in contrast to the manatee's more protected-water habitat), and with observations on captive dugongs (Kenny, 1967; Oke, 1967; Aung, 1967) indicating that they spend most of their time actively swimming, unlike the more sluggish manatees.

There are few reliable data on the swimming speeds of sirenians. Hartman (1971:128-131, 260-261) estimated the cruising speeds of wild Florida manatees at from 4 to 10 km/hr, with sprints up to 25 km/hr usually confined to 20-30 m and never sustained over 100 m. Stroke rates per minute varied from 20 when idling to 30-40 when cruising and 50 in full flight, stroke amplitude varying directly with rate. (A "stroke" is one complete undulation of the tail.)

The manatee data are not detailed enough to permit analyses like those done by Bainbridge (1958, 1961); however, they do confirm his observation (1958) that amplitude varies with frequency at frequencies below 3 to 5 beats per second, making the graph of speed against frequency describe a concave-upwards curve in this frequency range.

There are no data of comparable accuracy on dugong swimming speeds. Macmillan (1955:18) stated that traveling dugongs surface to breathe "about every hundred yards or so at about one-minute intervals or less," which indicates a cruising speed in the neighborhood of 6 km/hr. He (1955:

19) adds that "when towing a dinghy, a large dugong attains a speed of ten knots or more in its initial burst, and when towing a wood float it can go a great deal faster and fight longer." Similarly Jonklaas (1961:3) states: "It was not possible to estimate the maximum speed of a dugong, but judging from the two captives in a state of excitement, it would be safe to estimate a speed of at least 10 knots for short distances." Hence dugongs can easily exceed 18 km/hr. In the absence of evidence that their cruising or flight speeds are significantly different from those of manatees, we must conclude that the payoff from their more efficient body design is in the form of greater endurance not surprising if they normally live in more open waters (though they do prefer protected waters when these are available (Heinsohn, 1972:207)) and range over greater distances (though this is not proven).

Sirenians can, apparently by contraction of diagonally opposite sacrococygeus ventralis lateralis and longissimus muscles, oscillate their tail fins about the long axes of their bodies. Hartman (1971: 118, fig. 18) describes this action in manatees as used for steering, or counteracting roll or yaw when at rest. I have frequently observed a captive *Trichechus inunguis* at Steinhart Aquarium, San Francisco, continually and gently oscillating his tail in this manner, with an amplitude of several inches, while stationary and feeding; this may buffer against movements of the head, jaws, and flippers.

The large epaxial and hypaxial locomotor muscles are supplemented in the dugong by an unusual development of part of the subcutaneous muscles (cutaneus trunci). This consists of a thick mass on the underside of the tail, extending back to the level of the flukes, connected to the ischium (by a separate "ischiococcygeus"), continuous with the abdominal sheet that helps support the viscera, and inserting pinnately on a deep aponeurosis (attached to the tips of the chevron bones), which emerges to sheath superficially the sides of the tail. Its action is clearly to flex the tail, though whether it is important in normal swimming may be questioned. It is noteworthy that in the manatee the caudal extension of the cutaneus is much less developed. Nonetheless, manatees can flex their tails to an impressive degree (Murie, 1880, pls. 5, 7). Forward motion in manatees is initiated by an upstroke (Hartman, 1971:118); when frightened, dugongs can accelerate quickly from a standstill by a reverselobster-like backstroke of the sharply flexed tail (observed in the Ceylonese dugong; Mr. Ranil Senanayake, pers. comm.). This is in accord with the much greater size and strength of the epaxial versus the hypaxial muscles and the greater ventral than dorsal flexibility of the body. The small hypaxial muscle, which I have termed "flexor haemalis" (not noted in the manatee), may help to cock the flukes in this extreme flexed position and, perhaps, even produce a rudimentary "double lever" action on the upstroke. Although cetaceans are able, at least under passive manipulation, to attain this degree of flexion (Slijper, 1936:251), they do not seem to assume such a position nearly as habitually as do sirenians.

In normal swimming, as opposed to flexion of the body when at rest, the tail is, of course, not as strongly flexed, and the dorsal and ventral excursions are about equal in *Trichechus* (Hartman, 1971, fig. 17a) and doubtless also in *Dugong*.

The powerfully developed sphincter colli profundus pars auris also acts to flex the body, both by depressing the head and by pulling in opposition to the cutaneus trunci and rectus abdominis (through direct connection with the former, and via the sternum with the latter). Thus, there are two parallel and anastomosing linkages of ventral flexors running from the zygomatic arch of the skull to the underside of the flukes: (1) auris—cutaneus trunci, and (2) auris—sternum—rectus abdominis—ischium—ischiococcygeus—cutaneus trunci. How these function in the living animal is unknown.

In summary, sirenians closely parallel cetaceans in the design and development of their swimming apparatus; the arrangement of bones and muscles is fundamentally the same in the two orders and the same mechanical principles apply to both. The essential difference is that sirenians possess fewer of the refinements possible with this design, such as long tail tendons and special fluke elevator equipment, and are in general less advanced in this type of locomotor adaptation than any living cetacean. Their consequent lesser speed and endurance (also reflected in other features, such as low myoglobin content of muscles; Blessing, 1972) is not a handi-

cap as they are not active predators. Trichechids are in turn less well designed for swimming than the more active dugongids, and may approximate a structural stage through which the earliest dugongids passed.

FORELIMB MUSCLES

A survey of the literature reveals no evident differences in use of flippers between manatees and dugongs. In both animals they are used primarily as steering and balancing organs, and as a secondary means of locomotion (paddling for short distances forward, back, sideways, or upward; or "walking" along the bottom). They are not used as hydrofoils, as are cetacean flippers, but are held against the sides when swimming (except when in use for steering). They are probably not, as sometimes stated, used to uproot vegetation, but do at times serve to maneuver loose plant material to the mouth. They also perform a variety of actions such as scratching, mouth cleaning, supporting the body when resting on the bottom, and embracing other animals. (Representative references on this topic are Dexler and Freund, 1906; Jones, 1959; Jonklaas, 1961; Silas, 1961; and Hartman, 1971.) The extensive use of the flippers is reflected in the relatively high myoglobin content of the pectoral and forelimb muscles (Blessing, 1972).

The flipper is highly flexible and maneuverable; the wrist can be bent somewhat, and the digits to a lesser extent. When used in locomotion the flipper is always feathered (Hartman, 1971:123–127, figs. 20, 21), though, since the forearm bones cannot rotate (not even, it seems, in *Dugong*, where they are not fused), this is done with the shoulder joint. The elbow is free of the body, in contrast to the cetacean flipper, and on the whole the sirenian forelimb retains far more dexterity and is far less specialized than the cetacean.

The clearest differences between dugong and manatee forelimb anatomy are in the shoulder region. Skeletally, we may observe in the manatee scapula the striking forward prolongation of the acromion process and the backward-projecting tuber spinae; and in the humerus, the large lesser and small greater tuberosities, virtual absence of

a deltoid crest, and absence of a bicipital groove—all in contrast to the conditions in dugongids. The manubrium is proportionately wider in manatees than in *Dugong*.

With regard to the muscles, the serratus magnus is not divided into separate anterior and posterior parts in the manatee, though they are distinct in the dugong. The manatee's thoracic trapezius is quite different from the dugong's, passing directly and strongly backwards from the tuber spinae rather than almost transversely from the surface of the infraspinatus and the scapular cartilage. The deltoideus likewise arises only from the scapular spine. Both trapezius and deltoideus attach to the whole of the long acromion process; it is almost as if their scapular attachments are about the same length as in the dugong, but have shifted anteroventrally along the extended spine. The latissimus shares the insertion tendon of the teres major, not that of the pectoralis minor as in the dugong; the latter muscle in the manatee inserts more proximally. In the absence of a bicipital groove, the manatee biceps lies parallel and adjacent to the coracobrachialis; Murie (1872, 1880) in fact considered them a single muscle. The antebrachial muscles are not significantly different in the two animals, but the palmar muscles seem to be less developed and differentiated in the dugong, perhaps indicating less mobility of the digits.

Since the movements of the distal joints are similarly restricted in the two animals and flipper movements seem to involve mainly the shoulder joint, it is not surprising that whatever anatomical differences there are should be found, for the most part, proximally. But if we are ignorant of any difference in function between manatee and dugong flippers, how are we to explain these striking differences in form? I could not pretend to answer this question without much further study, but here is a first try at a solution: The divided serratus magnus of the dugong suggests greater specialization for moving the scapula in a parasagittal plane. On the other hand, the manatee's long acromion process suggests greater ability to abduct the forelimb. The height of the lesser tuberosity may indicate the same, as Howell suggested (1930:228). The more medial supraspinatus insertion would seem to rotate the palmar side of the manatee's forelimb forward (swinging the limb outward) during extension of the limb. The manatee's wider manubrium may indicate a more robust pectoralis major for adductive movements. So it could well be that the dugong's forelimb is used less in ways involving abduction and adduction than the manatee's. This may reflect the manatee's greater need to use the flippers in maneuvering in restricted bodies of water (cf. Hartman, 1971:123–124). Observations on the actions of wild dugongs should be made with this possible difference in mind.

HINDLIMB MUSCLES

No vestiges of hindlimb muscles have ever been identified in a sirenian. Dugongs are not known to ever possess remnants of limb bones attached to the pelvis, but vestigial femora are occasionally found in manatees, and these individuals may well have traces of leg muscles. These, however, would likely be impossible to homologize with those of normal quadrupeds; even in those mysticete whales where vestigial hind limbs are well developed, the muscles are too variable to be identified confidently (Struthers, 1893).

The pelvis in living sirenians, as in cetaceans, serves as an anchorage for several trunk, tail, and urogenital muscles, so it is unlikely that it would tend to be further reduced in the course of evolution.

Conclusion

The greatest desideratum in the study of sirenian functional anatomy (apart from redescription of the manatee's myology) is sound natural history data showing what the animals actually do in life—how they eat, how far and fast they swim, how and why they move all parts of their bodies. Without this firm connection to reality, our attempts at deciphering muscle "functions" cannot claim to be more than idle speculation. Our ability to analyze vertebrate myology is still rudimentary; we cannot yet confidently solve equations of muscle function in which one of the unknowns is the function itself. Without the guidance of the natural historian, the functional anatomist is only building castles in the air.

Addendum

After this paper had gone to press, Dr. Roger Saban graciously sent me a copy of his recent paper on "La musculature peaucière de la tête chez un jeune Lamantin du Sénégal (Trichechus senegalensis Link 1795; Mammisère, Sirénien)" (Zentralblatt für Veterinär Medizin, Reihe C: Anatomia Histologia Embryologia, 4(3):232-248, 1975). This paper sheds welcome light on differences in facial musculature between the African manatee, the West Indian manatee (described by Murie), and the dugong; of special interest in regard to the latter are the following points. Saban found two divisions of the sphincter colli profundus pars intermedia which are absent in the dugong: a ventral part posterior to the pars palpebralis and a dorsal part (zygomatico-labialis) fused with and anteriorly continuing the platysma beneath the palpebralis. He also found a "buccinator pars mentalis" which he homologized with Murie's mandibularis; however, as it arises in common with the buccinator pars longitudinalis from the pterygoid process rather than from the mandible (Saban, in litt., 26 May 1976), I prefer to identify it with my retractor labiorum. Saban observed the same attachments of the M. mentalis as I did in the dugong, which suggests that Murie's observation was in error. T. senegalensis contrasts with T. manatus in possessing the sphincter colli profundus partes intermedia ventralis et palpebralis and in several other points. Remarkably, the well-developed sphincter colli profundus ?pars auris found in both the dugong and the West Indian manatee does not appear in T. senegalensis; Saban (in litt., 26 May 1976) suggests that its homolog in the latter is the pars intermedia ventralis.

There remains a need for restudy of *T. manatus* to clarify the many doubtful points of Murie's description, and I hope to undertake a dissection of *T. inunguis* in the near future. Possible functional differences between the species of *Trichechus* are a wholly unexplored topic.

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List of Abbreviations

	Muscles	пт	Iliocostalis thoracis
		Inf	Infraspinatus
Abbreviations in parentheses on illustrations denote grooves		IntE	Intercostales externi
on bones fe	or tendons of muscles indicated; question marks	IntI	Intercostales interni
	denote doubtful identification	Into II-IV	Interossei
5.1.53		Intr	Intertransversarius coccygeus
AbD	Abductor digiti quinti	Isc	Ischiococcygeus
АЬР	?Abductor pollicis longus		
Ae	Aryepiglotticus	LaD	Latissimus dorsi
ArT	Arytenoideus transversus	LaN	Lateralis nasi
Au	Sphincter colli profundus	LeN	Levator nasolabialis
	?pars auris	LnC	Longissimus capitis
AuP	Auricularis profundus	LnD	Longissimus dorsi
AuS	Auricularis superficialis	LoCa	Longus capitis
_		LoCo ₁₋₃	Longus colli
В	Biceps brachii	Lu III-V	Lumbricales
Br	Brachialis		
Brc	Brachiocephalicus	M	Masseter
Brr	Brachioradialis	Mn	Mandibularis
Bu	Buccinatorius	Mnl	Maxillonasolabialis
		Mt	?Mentalis
Ch	Cephalohumeralis	My	Mylohyoideus
Cob	Coracobrachialis		
CoVe	Constrictor vestibuli	OAE	Obliquus abdominis externus
CoVu	Constrictor vulvae	OAI	Obliquus abdominis internus
CrD	Cricoarytenoideus dorsalis	OCa	Obliquus capitis caudalis
CrL	Cricoarytenoideus lateralis	OCr	Obliquus capitis cranialis
Crp	Cricopharyngeus	OOc	Orbicularis oculi
Crt	Cricothyroideus	OOr	Orbicularis oris
CuT	Cutaneus trunci		
D	Deltoideus	PaL	Palmaris longus
DAO		PlJ	Platysma pars jugularis
Di	Depressor anguli oris	PlP	Sphincter colli profundus pars palpebralis
Di	Digastricus	PIS	Platysma pars scapularis
ECR	Futancan comi radialia	PlT	Platysma pars temporalis
	Extensor carpi radialis	PMa	Pectoralis major
ECU EDC	Extensor carpi ulnaris	PMi	Pectoralis minor
	Extensor digitorum communis	PrT	Pronator teres
EDQ EP	Extensor digiti quinti	PtE	Pterygoideus externus
LI	Extensor pollicis brevis et longus	PtI	Pterygoideus internus
FCR	Flexor carpi radialis	Ptp	Pterygopharyngeus
FCU	Flexor carpi ulnaris		
FDP	Flexor digitorum profundus	RA	Rectus abdominis
FDQ	?Flexor digiti quinti brevis	RCI	Rectus capitis dorsalis
FDS	Flexor digitorum superficialis	1	?intermedius
FH	Flexor haemalis	RCMa	Rectus capitis dorsalis
Fr	?Frontalis		?major
x.≅ ·@0	. L. Tomang	RCMi	Rectus capitis dorsalis minor
Gg	Genioglossus	ReI	Retractor ischii
Gh	Geniohyoideus	ReL	Retractor labiorum
	, , , , , , , , , , , , , , , , , , , ,	Rh	Rhomboideus
He	?Hyoepiglotticus	RL	Rectus capitis lateralis
Hg	Hyoglossus		•
Нр	Hyopharyngeus	Sc	Scalenus
	/-L-m. / Beens	1	1000 to

			avagainital
SeC	Semispinalis capitis	eo	exoccipital
SeM	Serratus magnus	ep	epithelium of mouth cavity
SpA	Sphincter ani	es	esophagus or esophageal fibers
SpC	Sphincter colli superficialis	et	ethmoturbinal
Spl	Splenius	f	frontal
Stc	Sternocostalis	fm	foramen magnum
Stm	Sternomastoideus	g	glenoid facet (temporal condyle)
Stt	Sternothyroideus	gt	greater tuberosity of humerus
Styg1-3	Styloglossus	h	humerus
Styh	Stylohyoideus	il	ilium
Styp	Stylopharyngeus	is	ischium
Su	Subscapularis	j	jugal
Sup	Supraspinatus	jc	joint capsule
SVL	Sacrococcygeus ventralis lateralis	k	keratohyoid
SVM	Sacrococcygeus ventralis medialis	1	lumbar vertebra, transverse process
		lac	lacrimal
T	Temporalis	lg	deep cervical lymph glands
Ter	Teres major	lt	lesser tuberosity of humerus
TeV	Tensor veli palatini	m	mandible
Tha	Thyroarytenoideus	ma	position of mammary gland
Thh	Thyrohyoideus	mdf	mandibular foramen
Thp	Thyropharyngeus	mf	mental foramen
TrA	Transversus abdominis	ml	malleus
TrLa	Triceps brachii, lateral head	mx	maxilla
TrLo	Triceps brachii, long head	nm	nictitating membrane
TrM	Triceps brachii, medial head	1	
TrN	?Transversus nasi	nph	nasal pharynx
Trp	Trapezius	occ	occipital condyle
U	Urethralis	p	petrosal
C	Cictitans	pa	parietal
Z	Zygomaticomandibularis	pal	palatine
		pas	right posterior articulating surface of atlas
		pg	parotid gland
	OTHER STRUCTURES	ph	pharynx
		pm	premaxilla
a	anus	ps	presphenoid
ac	auricular cartilage	ptp	pterygoid process
af	antebrachial fascia	r	radius
ар	aponeurosis, superficial	r ₁₋₁₉	ribs
ar	arytenoid cartilage	rc	rib cartilage
b	basihyoid	S	symphysis
(\mathbf{bg})	bicipital groove	sac	sacral vertebra, transverse process
bo	basioccipital	sc	scapula
bs	basisphenoid	scc	scapular cartilage
by	blood vessels	sh	stylohyoid
bv(if)	blood vessels from infraorbital foramen	so	supraoccipital
bv(mf)	blood vessels from mental foramen	sq	squamosal
by & n	blood vessels and nerves	st	sternum
by & n(mdf)	blood vessels and nerves from mandibular	t	thyrohyoid
(/	foramen	tc	wall of tympanic cavity
c	cervical vertebra	th	thyroid cartilage
ca	caudal vertebra	to	tongue
ch	chevron bone	tr	trachea
cr	cricoid cartilage	trc	tracheal cartilages
d	diaphragm	ty	tympanic
	•		
e	epihyoid	u	ulna
eam	external auditory meatus	urp	upper rostral pad
eg	epiglottis	v	vulva
ejv	external jugular vein	vo	vomer
en	external nares	Z	zygomaticomandibularis insertion

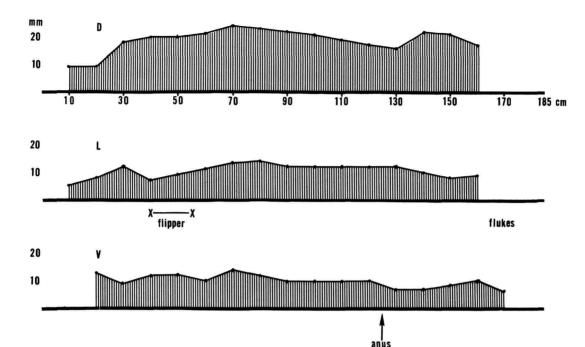


Figure 1.—Graph of skin thickness given in Table 2 (D = thickness in dorsal midline; L = thickness along side; V = thickness along ventral midline).

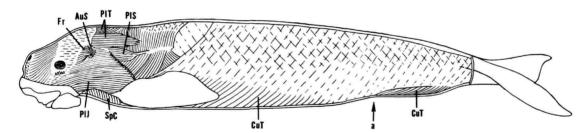


FIGURE 2.—Lateral view, dermal muscles and superficial aponeuroses; fascia over shoulder region removed behind pars jugularis of platysma. (For identification of other structures, see Figures 4 and 18.)

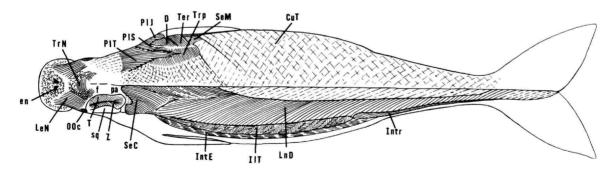
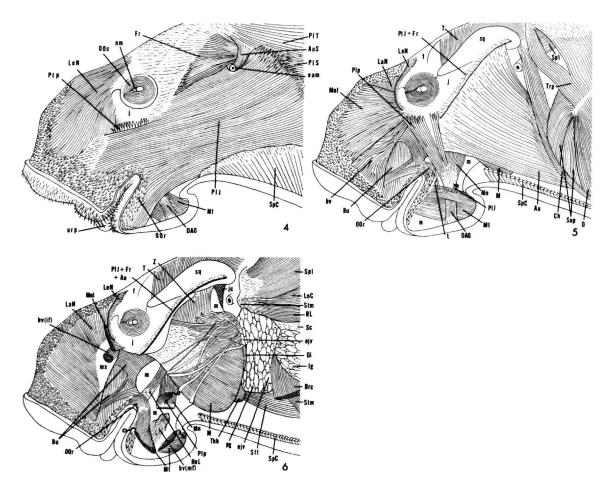


FIGURE 3.—Dorsal view, superficial muscles shown on right side of animal, deeper layer (with splenius, longissimus capitis, shoulder muscles, and forelimb removed) on left; superficial layer shown on both sides of snout.



FIGURES 4-6.—Lateral view of head: 4, superficial layer with facial bristles; 5, deeper layer (t = vestigial tendon of DAO); 6, deeper layer with shoulder girdle removed (note vessels and nerves crossing masseter).

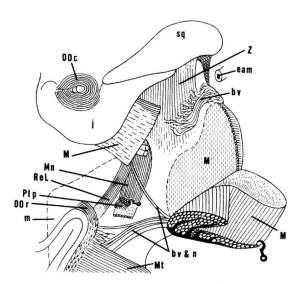


FIGURE 7.—Lateral view of jaw, masseter folded back to expose its insertion; position of external auditory meatus (eam) shown schematically; mandible (m) outlined.

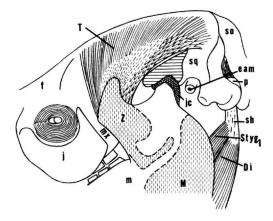
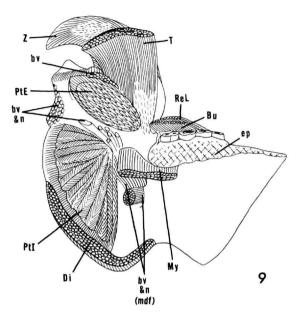
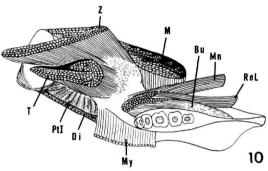


FIGURE 8.—Lateral view of jaw, zygomatic arch cut through jugal and root of zygomatic process, and arch removed to show temporalis, which is cut away from zygomaticomandibularis ventrally (M= masseter insertion, Z= zygomaticomandibularis insertion).



FIGURES 9-10.—Mandible (cut just behind symphysis) and attached structures: 9, medial view; 10, dorsal view.



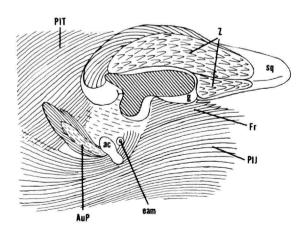
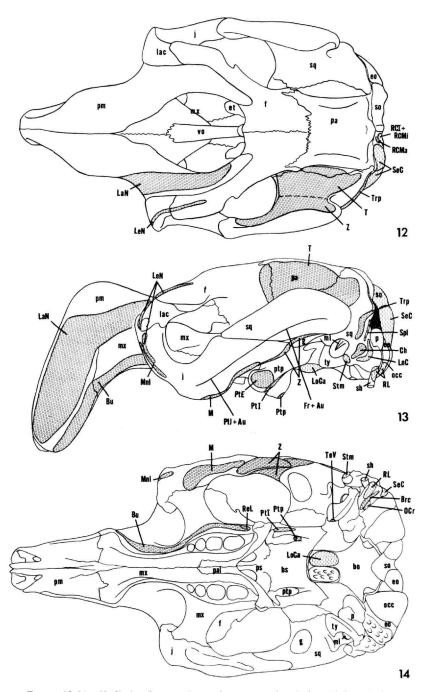


FIGURE 11.—Medial view, left zygomatic process (cut off at root) and attached dermal muscles (sphincter colli profundus pars auris omitted) (sq = zygomatic process of squamosal).



Figures 12-14.—Skull, showing muscle attachments: 12, dorsal view; 13, lateral view; 14, ventral view.

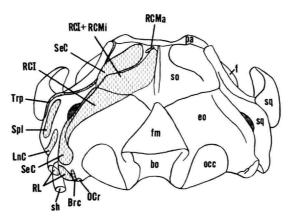
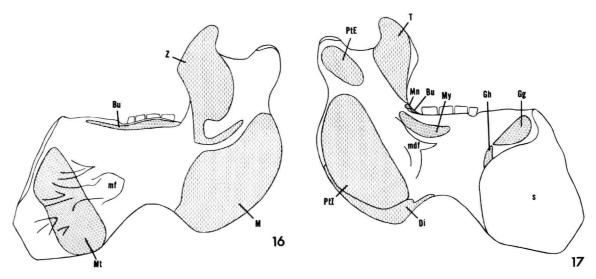
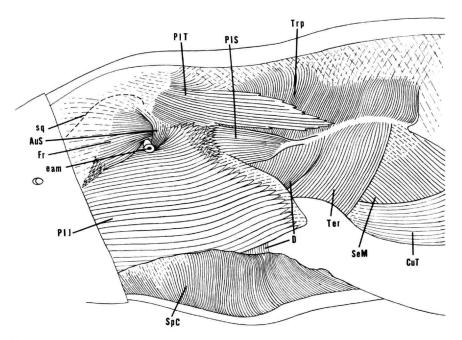


FIGURE 15.—Posterior view of skull, showing muscle attachments.



Figures 16-17.—Mandible, showing muscle attachments: 16, lateral view; 17, medial view.



 $\label{eq:figure 18} \textbf{Figure 18.--Lateral view of shoulder region, showing superficial muscles; fascia removed behind pars jugularis of platysma (sq = outline of zygomatic process of squamosal).}$

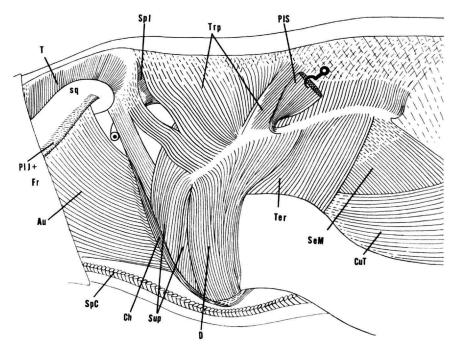


FIGURE 19.—Lateral view of shoulder region, most of superficial dermal muscles removed.

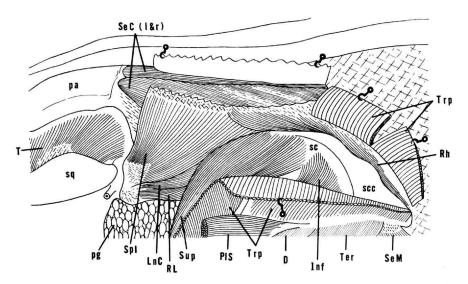


FIGURE 20.—Dorsolateral view of neck and shoulder region; platysma, cephalohumeralis, and anterior trapezius removed, splenius-rhomboideus aponeurosis cut and folded back to show left and right semispinalis capitis.

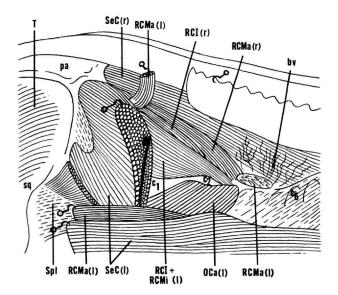


FIGURE 21.—Dorsolateral and somewhat posterior view of deep dorsal neck muscles, left semispinalis capitis and rectus capitis dorsalis major cut (latter in two places) and pulled away. Note asymmetrical arrangement of left and right rectus muscles.

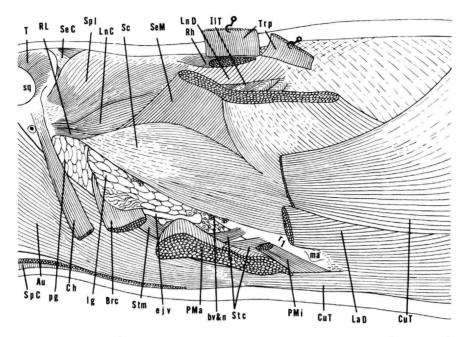


FIGURE 22.—Lateral view of neck and shoulder region, shoulder girdle and limb removed; position of mammary gland (ma) indicated.

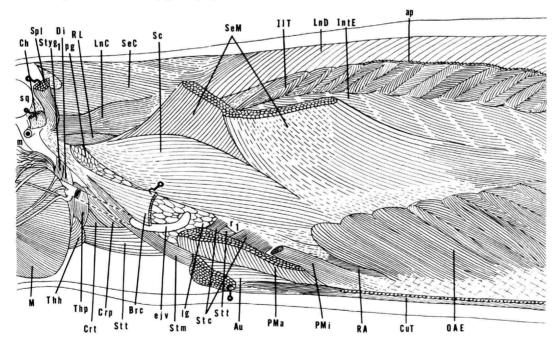


FIGURE 23.—Lateral view of neck and shoulder region, deeper dissection than in Figure 22; latissimus dorsi and most of cutaneus muscles and parotid gland removed; deep attachment of superficial aponeurosis (ap) cut; part of parotid gland (pg) shown.

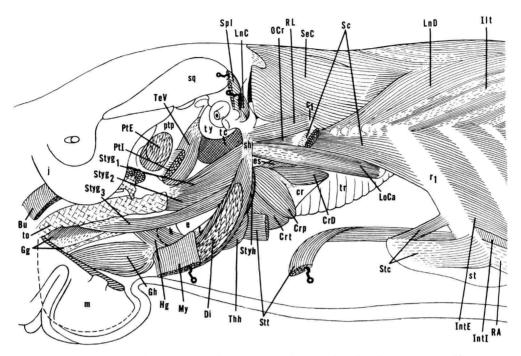


FIGURE 24.—Lateral view, deep dissection of tongue, throat, and neck region; sternomastoideus, pectorales, glands, and most of scalenus and mandible removed. Deep fibers of scalenus (split longitudinally) shown attaching to rib; keratohyoid (k) outlined; anterior end of mandible (m) outlined ($c_1 = atlas$).

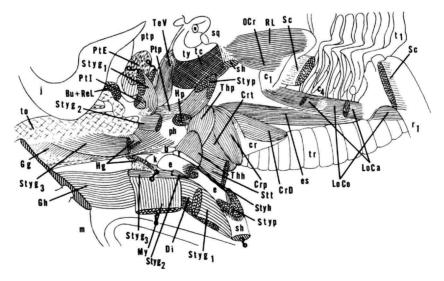


FIGURE 25.—Lateral view, deep throat muscles; hyoid arch cut through stylohyoid and folded down. Deep fibers of scalenus shown attaching to rib; cervical vertebrae exposed; mandible (m) cut (t_i = first thoracic vertebra).

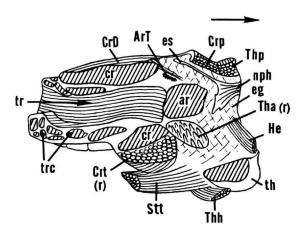


FIGURE 26.—Parasagittal section of larynx (cut just forward of epiglottis and just behind bifurcation of trachea), slightly to right of midline; anterior end to right. Parts of right cricothyroideus and thyroarytenoideus (cut obliquely) shown; right arytenoid cartilage (ar), nasal pharynx (nph) with longitudinal folds of lining, and trachea (tr) with longitudinal striations of lining shown.

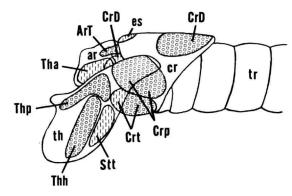


FIGURE 28.—Diagrammatic left lateral view of laryngeal cartilages, showing muscle attachments. The epiglottis is not cartilaginous in sirenians (es = attachment of esophageal fibers).

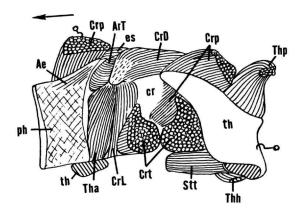


FIGURE 27.—Left lateral view of larynx, thyroid cartilage cut near midline, and left ala, with attached muscles, turned back; pharynx (ph) enclosing epiglottis.

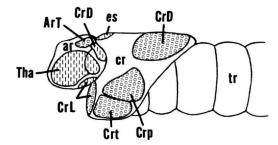
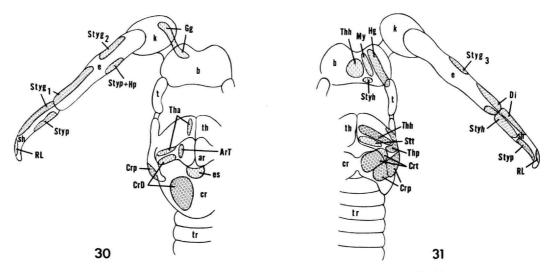
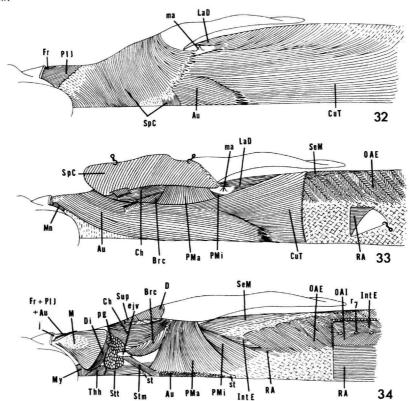


FIGURE 29.—Diagrammatic left lateral view of laryngeal cartilages, showing muscle attachments, with thyroid cartilage removed.



FIGURES 30-31.—Diagrammatic views of laryngeal cartilages and left half of hyoid apparatus, showing muscle attachments: 30, dorsal view (es = attachment of esophageal fibers): 31, ventral view.



FIGURES 32-34.—Ventral view of left throat and chest region: 32, superficial layer; 33, deeper layer than Figure 32 (note fibers of sphincter colli superficialis arising from sphincter colli profundus pars auris, and part of external rectus sheath folded back to expose rectus abdominis); 34, deeper layer than Figure 33.

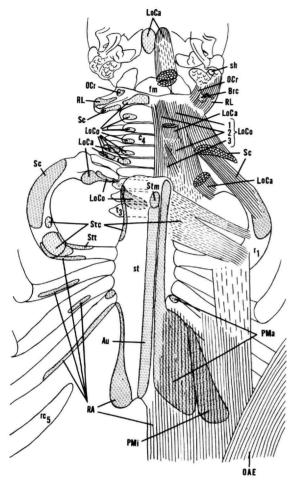


FIGURE 35.—Diagrammatic ventral view of neck and chest, showing muscle attachments (except pectorales, cutaneus capitis, and sternomastoideus) on animal's right side and deep neck and chest muscles on left. Centra of thoracic vertebrae and origin of longus colli thereon shown by dashed outlines. Deep fibers of scalenus shown attaching to rib. Longus colli divisions are not very distinct. Note origins of pectorales from surface of rectus abdominis. In most dugongs only three ribs attach to sternum; this specimen had four (sh = stylohyoid cut; t₁ = third thoracic vertebra).

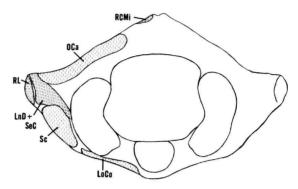


FIGURE 36.—Posterior view of atlas, showing muscle attachments.

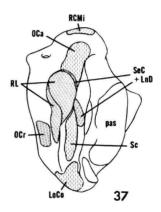


FIGURE 37.—Posterolateral view of atlas, showing muscle attachments.

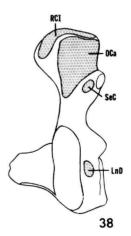


FIGURE 38.—Lateral view of axis, showing muscle attachments.

FIGURE 41.-Anterior view of

left first rib, showing muscle

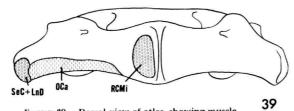


FIGURE 39.—Dorsal view of atlas, showing muscle attachments.

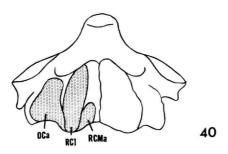


FIGURE 40.—Dorsal view of axis, showing muscle attachments.

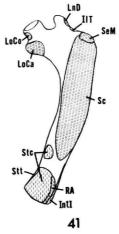
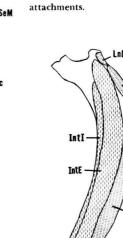
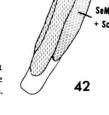


FIGURE 42.—Anterior view of left second rib, showing muscle attachments.





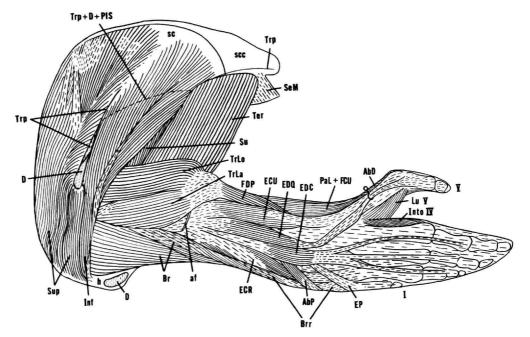


FIGURE 43.—Lateral view of forelimb; trapezius and deltoideus removed, but attachments shown. Extensor digiti quinti tendon pulled back to show its proximal insertion; cut edge of antebrachial fascia (af) removed. (Note: In Figures 43, 44, 46, 47, the limb is shown in the position it had assumed in the fixed specimen; whether it could have been this strongly flexed in the living animal is not certain.)

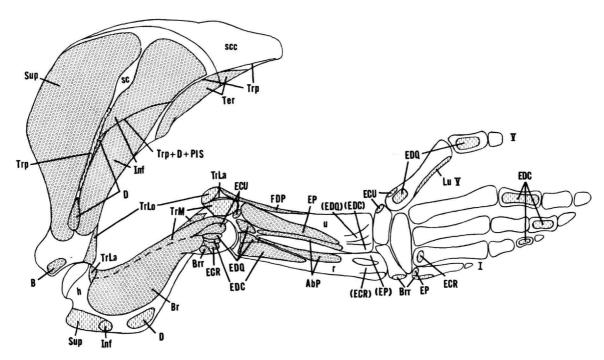


FIGURE 44.—Lateral view of limb bones, showing muscle attachments.

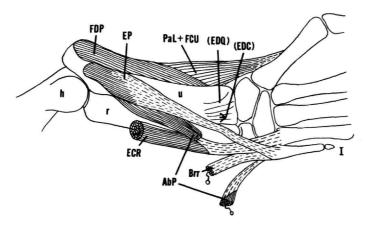


FIGURE 45.—Lateral view, deep antebrachial muscles. Retracted distal part of abductor pollicis longus shows the muscle's deep side. Abbreviations in parentheses denote grooves on ulna for tendons of muscles indicated; extensor digitorum communis groove faintly divided for the tendon's three incipient divisions to digits II-IV.

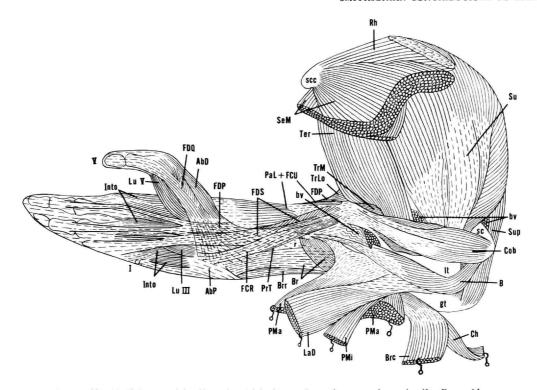


FIGURE 46.—Medial view of forelimb; brachial plexus of vessels removed proximally. Deep sides of latissimus dorsi and pectorales visible.

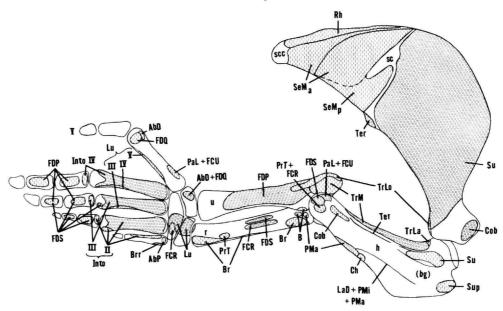


Figure 47.—Medial view of limb bones, showing muscle attachments. Insertions of anterior $(SeM_{\tt p})$ and posterior $(SeM_{\tt p})$ serratus magnus distinguished.

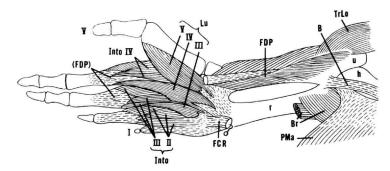


FIGURE 48.—Medial view, deep antebrachial and palmar muscles. (FDP = grooves on joint capsules for flexor digitorum profundus tendons to digits III and IV).

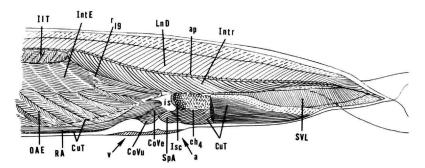


FIGURE 49.—Lateral view of posterior trunk and tail, most of cutaneus trunci and outer rectus abdominis sheath removed. Dashed line crossing obliquus abdominis externus shows outline of muscular part of cutaneus trunci; behind anus, cutaneus is shown cut in sagittal plane; and farther aft it is shown intact except for removal of dorsal part of its aponeurosis; deep attachment of superficial aponeurosis (ap) cut; some dugongs have only 18 ribs; this specimen had 19.

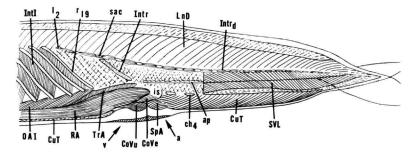


FIGURE 50.—Lateral view of posterior trunk and tail, second layer removed from ventral side. Deep bundles (Intr_d) and origin on pelvis of intertransversarius coccygeus shown. Caudal part of cutaneus trunci cut in sagittal plane, and its aponeurosis removed posteriorly to expose sacrococcygeus ventralis lateralis. Latter is triangular in cross-section, the apex of the triangle forming the ridge shown as a longitudinal line aligned with the cut edge of an aponeurosis (ap); this marks the ventral extent of the intertransversarius, which arises from aponeurosis on surface of sacrococcygeus ventralis lateralis.

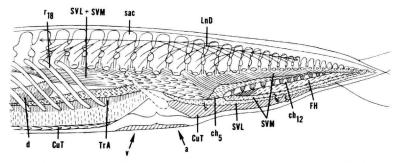


FIGURE 51.—Lateral view of deep ventral muscles of posterior trunk and tail. Structure of longissimus dorsi shown schematically; both origins and insertions continue forward and back in addition to the few attachments shown. Position of pelvis shown by dashed outline. Genital and anal muscles omitted; see Figure 52. Posterior part of sacrococcygeus ventralis lateralis cut away from sacrococcygeus ventralis medialis and removed; aponeuroses of both cut and turned down to expose chevrons and flexor haemalis; diaphragm (d) cut and removed dorsally to expose sacrococcygeus.

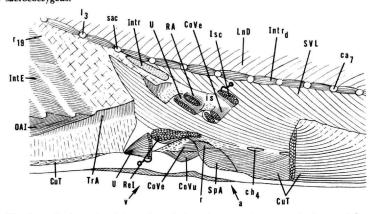
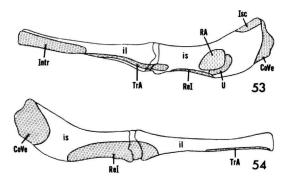


FIGURE 52.—Lateral view of pelvic and genital region; structures attached to pelvis cut and pelvis pulled back and upward. Deep bundles (Intr_d) and origin on pelvis of intertransversarius coccygeus shown. Most of rectus abdominis and more superficial muscles removed, inner rectus sheath exposed. Cutaneus trunci cut in sagittal plane ahead of fifth chevron bone, but shown intact farther aft except for removal of dorsal part of its aponeurosis. Note part of transversus abdominis still attached to pelvis (r = longitudinal muscle fibers of rectum).



FIGURES 53-54.—Left pelvis, showing muscle attachments: 53, lateral view; 54, medial view.

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